

UPPER JURASSIC RHYNCHONELLID
BRACHIOPODS FROM NORTHWESTERN
EUROPE



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By ALAN CHILDS

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SYNOPSIS

The major part of this study comprises a systematic revision of most of the Upper Jurassic rhynchonellids of northwestern Europe. Thirty-five species belonging to the genera *Monticlavella*, *Lacunosella*, *Rhynchonella*, *Thurmannella*, *Acanthothiris*, *Acanthorhynchia*, *Somalirhynchia*, *Septaliphoria*, and *Torquirhynchia* gen. nov. are described. By using serial sectioning and acetate peel techniques, the internal structures of all but the rarest species have been investigated and the majority of these are described and figured for the first time. New taxa include six species, a subgenus, and a genus.

Observations on ecology and distribution are given with the specific descriptions and separate sections are also included dealing with these aspects at generic level.

INTRODUCTION

IN contrast to the many monographs describing the complete faunas of small areas, this study consists of the examination of a single order, the Rhynchonellida, over a wider region ; the author considering that this approach provides a much better basis for taxonomic as well as ecological and distributional studies. The rhynchonellid brachiopods are a morphologically diverse group and, although not numerous in the Upper Jurassic of the British Isles, they colonised a wide range of habitats in N.W. Europe during this period.

Although most of the species described have been previously figured, this is the first attempt to give such a comprehensive account of these faunas and to clarify their synonymies. It is interesting to note in this connection that the French literature abounds with Orbigny and Lamarck species, the German with those of Schlotheim, Oppel and Quenstedt while many British authors have relied on Sowerby and Davidson. By making a palaeontological study on a wider geographical basis than is usually attempted, it is hoped to reduce the number of species confined by national boundaries. It is considered that the other major justification for attempting to study a group over a relatively wide geographical area is that in considering evolutionary lineages this helps to eliminate any local distortion caused by migration and the general imperfection of the fossil record.

Although essentially work has been confined to taxa within the Upper Jurassic, certain species and genera from lower stratigraphical levels have been investigated where this was thought necessary. The type species of *Acanthorhynchia*, namely *A. panacanathina*, from the Bajocian has thus been included and similarly a study was made of *Acanthothiris spinosa* in order to determine the justification for splitting the spinose forms into separate genera.

Previous research

Although no previous author has attempted to produce such a comprehensive monograph of this group of rhynchonellids, there have been numerous descriptions and figures published over the last two hundred years. As there are relatively few rhynchonellids in the British Upper Jurassic rocks, most of the works referred to are by continental authors.

Linnaeus (1767) described only one of the species discussed below, namely *Acanthothiris spinosa*; this species was also the subject of the first figure to which reference is made, Knorr and Walch (1769). This appears to be the only recognisable eighteenth century description of a Middle or Upper Jurassic rhynchonellid. Of the workers of the early part of the nineteenth century, the most important were Schlotheim (1813, 1820), Zieten (1830-33) and, to a lesser extent, Lamarck (1819). The paucity of British Upper Jurassic material meant that the Sowerbys figured only one species—*Torquirhynchia inconstans*. Fischer de Waldheim's paper of 1809 must also be mentioned as this introduced the genus *Rhynchonella*. The major nineteenth century French work was undoubtedly d'Orbigny's (1850) "Prodrome", but this lost much of its potential value through lack of illustrations.

From about 1850 until the beginning of the present century several eminent palaeontologists produced many of the monographs still regarded as standard works. These writers included Davidson, who described and figured all the then known British brachiopods, Eudes-Deslongchamps, who produced numerous well illustrated papers on the brachiopod faunas of Normandy and elsewhere and Loriol and Haas who produced similar comprehensive works on the French and Swiss Jura. Many of the monographs of these authors set standards which have seldom been surpassed. Mention must also be made of the writings of Quenstedt (1851-52), which culminated in his magnificent work "Die Brachiopoden" (1868-71), still the most complete

illustrated account of European brachiopods. Apart from these, there are also numerous papers and monographs dealing with smaller areas such as those of Struckmann (1878) on the region of Hannover and Rothpletz (1886) on the Vilser Alps. The latter, while strictly outside the area under consideration, includes important discussion on the higher taxonomy of many of the species described.

UPPER JURASSIC ZONES AND STAGES	
nodiger	UPPER VOLGIAN
subditus	
fulgens	
giganteus	LOWER VOLGIAN
gorei	
albani	
pallasioides	
rotunda	
pectinatus	
wheatleyensis	
Subplanites spp.	
Gravesia spp.	
pseudomutabilis	
mutabilis	
cymodoce	
baylei	
pseudocordata	OXFORDIAN
transversarium	
cordatum	
mariae	

FIG. 1. The nomenclature of the Upper Jurassic zones and stages used in this study, following the recommendation of the British Mesozoic Committee as reported by Ager (1964).

During the present century there has been relatively little investigation of the Upper Jurassic rhynchonellids. Buckman (1918), as part of his "Burma Memoir", completely revised the taxonomy of the Jurassic rhynchonellids but this revision was largely based on Lower and Middle Jurassic British material and few of the species here described can be attributed to his genera. With regard to Buckman's work, Ager (1956) wrote, "His (Buckman's) classification is not now accepted, his terminology is unnecessarily complex and his emphasis in description is frequently misdirected". In 1917 Rollier produced his "Synopses" in which he attempted to elucidate the synonymies and redefine all Jurassic brachiopod species. While this work contains many useful suggestions, it was apparently undertaken without any reference to original specimens and consequently contains many misconceptions as a

result of referring to figures and descriptions which were inadequate in the first place. In 1920 Leidhold published a paper in which he proposed the genus *Septaliphoria* and two subgenera within it, namely *Thurmannella* and *Blochmannella*. Although the descriptions of the type species were inadequate, the names *Septaliphoria* and *Thurmannella* have since been widely used as a result of the lack of generic names at this level.

Probably the most notable contribution to the subject was Wiśniewska's (1932) monograph on the Upper Jurassic rhynchonellids of Poland. In that work she proposed the genera *Monticlarella*, *Lacunosella* and *Septocurella* and in publishing the first transverse serial sections of many of the rhynchonellids of this age made a major advance in their study. The use of transverse serial sections was well known to several authors of the last century, notably Bittner and Rothpletz, but the technique was allowed to lapse until its use by Wiśniewska and its application was not widely publicised until Muir-Wood's paper in 1934. In common with virtually all the other works previously mentioned, Wiśniewska gave no details of lithology or associated fauna and very little information about relative abundance and distribution.

Since Wiśniewska, the only major work devoted to the Upper Jurassic brachiopods has been Makridin's (1964) study of the faunas of the Russian Platform. In this work Makridin was seriously handicapped by a lack of comparative material from the classic areas of N.W. Europe and, as a result, many of his assignments and conclusions are considered to be doubtful. Brief diagnoses of all the Mesozoic genera are to be found in Makridin (1960) and Ager (1965*b*). The ecological aspects of the Mesozoic brachiopod faunas have recently been discussed by Makridin (1964) and Ager (1965*a*).

II. ECOLOGY

The environments colonised by the rhynchonellids during the whole of the Mesozoic were discussed in detail by Ager (1965*a*). In that paper seven different habitats were recognized namely: (1) very shallow water sea floors, (2) sublittoral, sand grade sea floors without reefs, (3) sea floors in the vicinity of reefs, (4) shallow, non-depositional sea floors, (5) sublittoral, mud-grade sea floors, (6) deeper (? bathyal) mud-grade sea floors, (7) floating weed, and the adaptations shown by the Mesozoic brachiopods to each of them described. Within the area described by the present author, however, not all these environments appear to be present as the region was largely covered by a relatively shallow shelf sea. As far as they have been elucidated, the environments colonised by the rhynchonellids during the Upper Jurassic in northwestern Europe are as follows:

(a) *Sandy, near-shore environments.*

This facies is well developed in the lower and middle Oxfordian around the northern rim of the Paris Basin; a similar environment was also present in much the same area during lower Callovian times and, while this is strictly outside the stratigraphical limits of this study, it is discussed for comparison. The formations representing this environment at these times were the "Terrain à Chailles" and

the "Varians Schichten" respectively. Both of them are sandy limestones, although they differ in that the former contains nodular layers of chert. Each of these formations contains an abundance of rhynchonellids and in each of them two markedly different types are present. The two rhynchonellids occurring in the "Terrain à Chailles" are *Septaliphoria arduennensis* (Oppel) and *Thurmannella obtrita* (Defrance). The former is much the larger and in having coarse ribs, a strong beak and a large pedicle opening was obviously adapted to a high energy environment. The much more abundant *T. obtrita* has relatively much finer ribbing and a very thin test, although it too has a well developed pedicle opening. Within the "Varians Schichten" the rhynchonellids are of much the same size and occur in similar proportions. In this case the larger is *Acanthothiris spinosa* (Linnaeus) and the smaller species is *Ivanoviella alemanica* (Rollier). The former, like *S. arduennensis*, tends to occur singly rather than the large groups in which *T. obtrita* and *Ivanoviella alemanica* are found. The latter species closely resembles *T. obtrita* externally except that it has stronger ribs and a more limited posterior smooth area. It is suggested that the similarity of environments in which *A. spinosa* and *S. arduennensis* are found, and the fact that the latter species is obviously adapted to living an attached existence in such conditions is strong evidence for regarding the spines of *A. spinosa* as an anchoring mechanism, especially as its pedicle atrophied during ontogeny. This view is in contrast to that of Rudwick (1965) who considered these spines to be of a sensory nature. It is thought that the smaller, thinner shelled *T. obtrita* and *I. alemanica* probably lived attached to algae. This idea is supported by the presence of the relatively large pedicle opening, while the very thin shell of *T. obtrita*, as seen in silicified material, would appear to preclude its survival on the bottom in such numbers in a high energy environment. However, it is always possible that they lived in sheltered niches within this environment.

The same type of environment is suggested for the deposition of the Lower Calcareous Grit as seen on the Yorkshire coast. In that area *Thurmannella* is again abundant but any larger rhynchonellids appear to be very much rarer although Mr. E. F. Owen (personal communication, 1966) states that he has found *Septaliphoria* on Filey Brigg. The material described below as *S. paucicosta* sp. nov. came from inland localities but it is not known whether or not the species is associated with *Thurmannella* sp. The amount of material in the B.M. (N.H.) would suggest that *S. paucicosta* is very common at least at its type locality of Hutton Bushel.

The nearest comparable lithology and environment in the Kimmeridgian is provided by the Alt-na-Cuile Sandstone of Sutherland. This latter formation is a decalcified sandstone containing a rich fauna of rhynchonellids preserved as casts. As far as can be determined, given the poor preservation, this seems to be a coarse ribbed form closely comparable with *Septaliphoria* but as its internal structures are not preserved its exact relationship cannot be determined. This latter species is described below under the name *Septaliphoria* (?) *septentrionalis* sp. nov. The Abbotsbury Ironstone (Kimmeridgian) of Dorset may also represent this type of environment. Here again, the fauna includes poorly preserved rhynchonellids doubtfully ascribed to *Septaliphoria* (?) *hudlestoni* (Rollier).

Ager (1965a) suggested that the strongly uniplicate rhynchonellids such as *Homoeorhynchia acuta* and *Rhynchonella loxiae* were characteristic of sand grade, sublittoral sea floors. However, it is not thought that all species of the genus *Rhynchonella* lived in this type of environment as at least two of them, namely, *R. subvariabilis* and *R. riveleensis*, occur in clays or marls. It appears from the relatively limited information available that the earlier species attributable to *Rhynchonella* s.s. are always found in such lithologies and that it is not until Volgian times that the genus is found in a more sandy facies which presumably represents a higher energy environment. Makridin (1964), who gives the range of *Rhynchonella* as late Kimmeridgian—early Cretaceous, states that, "members of the genus are most widespread in the shoaly facies of a sandy and sandy-clay sublittoral". If the above information is correct, then it is interesting to note that the genus became much more morphologically diverse on colonising the higher energy environment. It is possible that *Rhynchonella* only colonised these environments on the extinction of such genera as *Septaliphoria*. In order to account for the occurrence of *R. subvariabilis*, Ager suggested a pelagic mode of life and it is thought that such a mode of life would also best account for the occurrences of the earlier species of the genus such as *R. riveleensis* and *R. triplicosa*, this is discussed further below.

(b) *Sea floors in the vicinity of reefs.*

While Ager (1965a) referred exclusively to the forms encountered in the vicinity of hermatypic coral reefs, within the Upper Jurassic, it is possible to subdivide this environment according to whether the reefs are coral or sponge. The greatest development of sponge reefs is found in the regions of Swabia and Franconia where they flourished from middle Oxfordian to, at least, lower Volgian times. The rhynchonellid fauna associated with these reefs is very distinctive and consists almost entirely of species of the genus *Lacunosella*. The incidence of sponges with *Lacunosella* spp. is such as to suggest that the rhynchonellids were actually dependent on them. Middlemiss (1962) has recorded rhynchonellids within the folds of *Rhaphidonema* in the Lower Greensand at Faringdon, Berkshire, and this may possibly be a commensal relationship; unfortunately, details of the rhynchonellids were not given. It has also been suggested (Ager, 1965a) that *Orbirhynchia* of the Upper Cretaceous adopted a similar mode of life and it may be significant that both the latter genus and *Lacunosella* possess the distinctive blade-like falcifer crura. Apart from *Lacunosella*, the only other rhynchonellid genera known to occur in the sponge reef facies are *Acanthorhynchia* (*Echinirhynchia*) and *Monticlarella*; these may well have been pelagic forms and are discussed further below.

The important factor in determining the distribution of the lacunosellids would seem to be the presence of sponges and whether these were living as reef assemblages, loose groups or "lenses" mattered little. While the greatest abundance and variety of lacunosellids is found in the sponge reefs of Germany where sponges were the dominant feature of the fauna during the Upper Jurassic, in the southern French Jura *L. arolica* occurs in calcareous shales with only isolated sponges.

The areas around the coral reefs appear to have been colonised by two genera. The more distinctive externally is *Torquirhynchia* gen. nov., which comprises a

series of strongly asymmetrical species, as typified by *T. inconstans* (J. Sowerby) from the Kimmeridge Clay. The reason for this somewhat bizarre development is not understood ; however, it is interesting to note that the individuals concerned can be inverted and still retain the same form of anterior commissure. This is particularly obvious in the more globose specimens of *T. inconstans* in which the brachial valve was inflated to such an extent that the pedicle must have atrophied. Given the subspherical appearance of these inflated specimens, their lack of a pedicle and the fact that they apparently lived in a high energy, perireefal environment, it seems reasonable to assume that the development of asymmetry was related to these facts. That *Torquirhynchia* species can be inverted and still retain the same form of anterior commissure may possibly have been of advantage in that, as the right and left halves of the mantle cavity are physiologically independent (Orton, 1914), at least half of the lophophore system would have a water intake well clear of the bottom.

With the exception of *T. cf. T. astieriformis*, which was collected from around a small sponge reef, the genus has always been found associated either with corals or with "reef" limestones. *Torquirhynchia* seems to be completely absent from the sponge reef facies of the Swabian and Franconian Alb ; *T. speciosa* is found in the Kelheim area but the "Dicerat Kalk" in which it occurs has much closer affinities with the fauna of the Stramberk Limestone of Czechoslovakia.

Apart from *Torquirhynchia*, the only other genus to have colonised the areas around coral reefs is *Somalirhynchia* Weir. *S. moeschi* (Haas), which occurs widely in the central French Jura, is always associated with corals according to M. Enay (personal communication, 1965) and this was certainly so at the one locality where it was collected by the author. It is considered that the presence of corals in the Kimmeridgian Boulder Beds of Sutherland is significant in accounting for the occurrence of *S. sutherlandi*. This occurrence of *S. sutherlandi* is discussed in some detail under the specific description. It must be stressed that both *Torquirhynchia* and *Somalirhynchia* appear to be strictly perireefal. Elliot (1950) has suggested that the absence of brachiopods within reefs is probably a result of the coral polyps eating the brachiopod larvae.

(c) *Sublittoral, muddy sea floors.*

This is the remaining major environment in which rhynchonellids have been collected. As stated by Ager, it seems reasonable to assume that this is a deeper water facies than those discussed above, but this need not be so and the present writer would agree that the grain size of the substratum seems to be more important than the actual depth. With regard to this latter point, at various localities in the southern French Jura *Lacunosella arolica* occurs in a marly facies. However, as stated above, it is invariably associated with sponges and it is considered that these represented the substrate as far as the lacunosellids were concerned and consequently the presence of sponges is the determining factor rather than sediment or depth.

Other genera which occur in this environment include *Rhynchonella*, *Thurmannella*, *Echinirhynchia* and *Monticlarella*. Of these it is suggested that forms such as *T.*

obtrita from the "Rengeri Marl" and *R. rivelensis* and *R. subvariabilis* from the upper Oxfordian and upper Kimmeridgian respectively were probably attached to algae during life. This is suggested as the normal mode of existence but does not preclude occasional specimens being drifted considerable distances and thus accounting for the occurrence of rare species such as *subvariabilis*, as suggested by Ager. *T. obtrita* and *R. rivelensis* occur in such abundance that it seems unlikely that they



FIG. 2. The solid black area represents the outcrop of the Callovian-Volgian; this information is taken from the map commissioned by the World Geological Congress of 1881. A generalized palaeogeography of the Oxfordian-Kimmeridgian (after Kuhn, 1953) is shown with the land areas ornamented with crosses.

taxa concerned, suggest that they were attached to algae or sponges and consequently easily drifted long distances. While the normal mode of life may well have been the same as that of *Lacunosella*, the small size and delicate nature of the test obviously made it much easier for them to be transported over considerable distances and account for their appearance in such a diverse range of habitats.

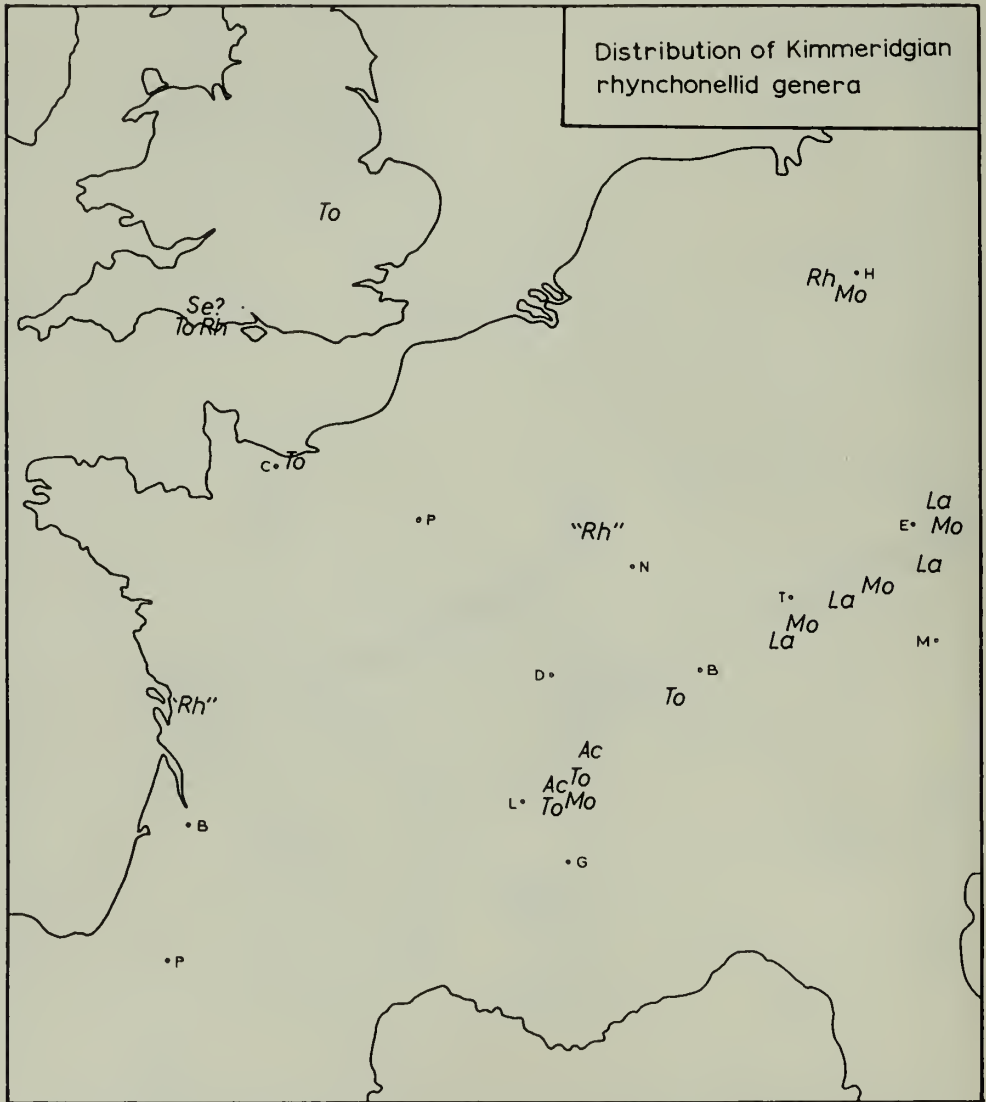


FIG. 4. Ac=*Acanthorhynchia*; La=*Lacunosella*; Mo=*Monticlavella*; Rh=*Rhynchonella*; "Rh"=*Rhynchonella*; Se?=*Septaliphoria*?; To=*Torquirhynchia*.

GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTION

Details of the distribution of individual species are given in the systematic part of this study but text-figs. 3-5 have been included to summarise the distribution of the genera. These figures are based on information obtained from field observations, museum collections and literature. It is considered that the distribution is largely controlled by facies and substrate, as shown by the occurrence of *Septaliphoria* and *Lacunosella*.

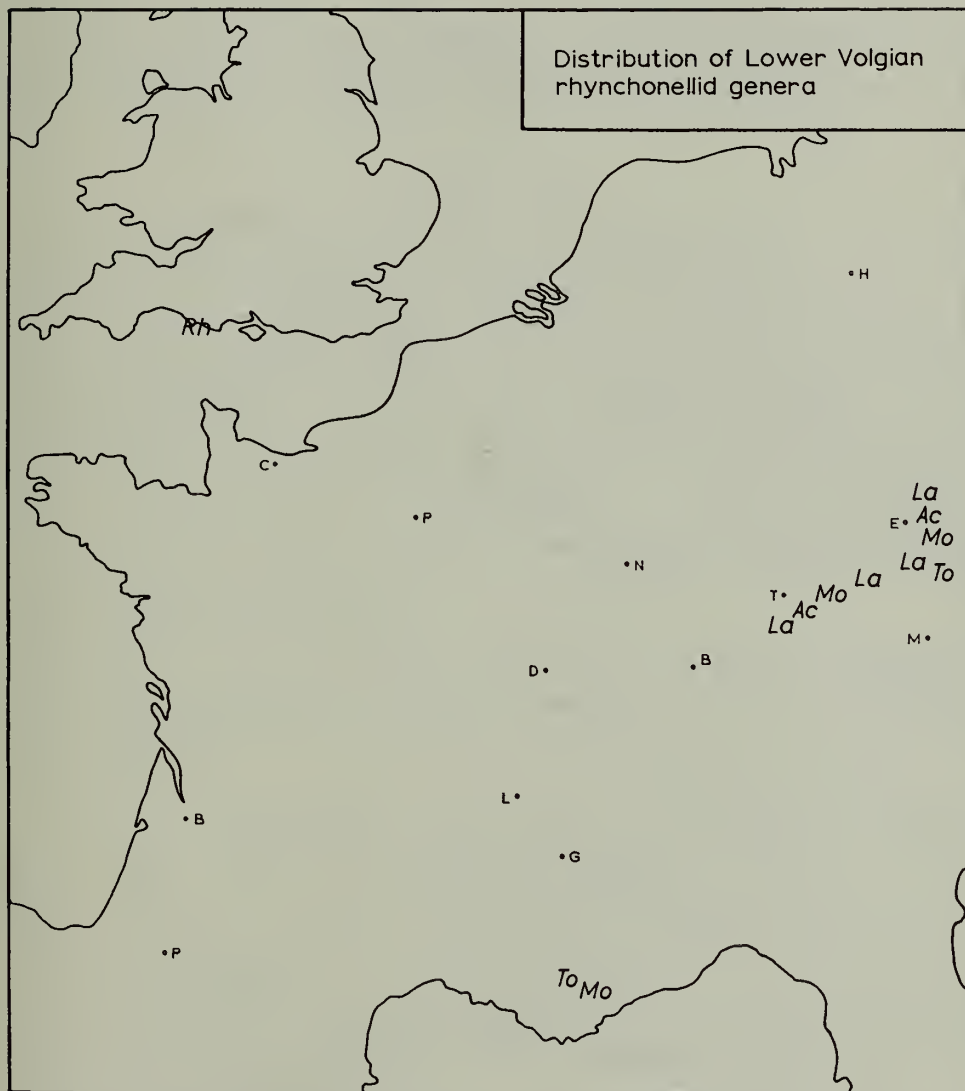


FIG. 5. Ac=*Acanthorhynchia* ; La=*Lacunosella* ; Mo=*Monticlarella* ; Rh=*Rhynchonella* ; To=*Torquirhynchia*.

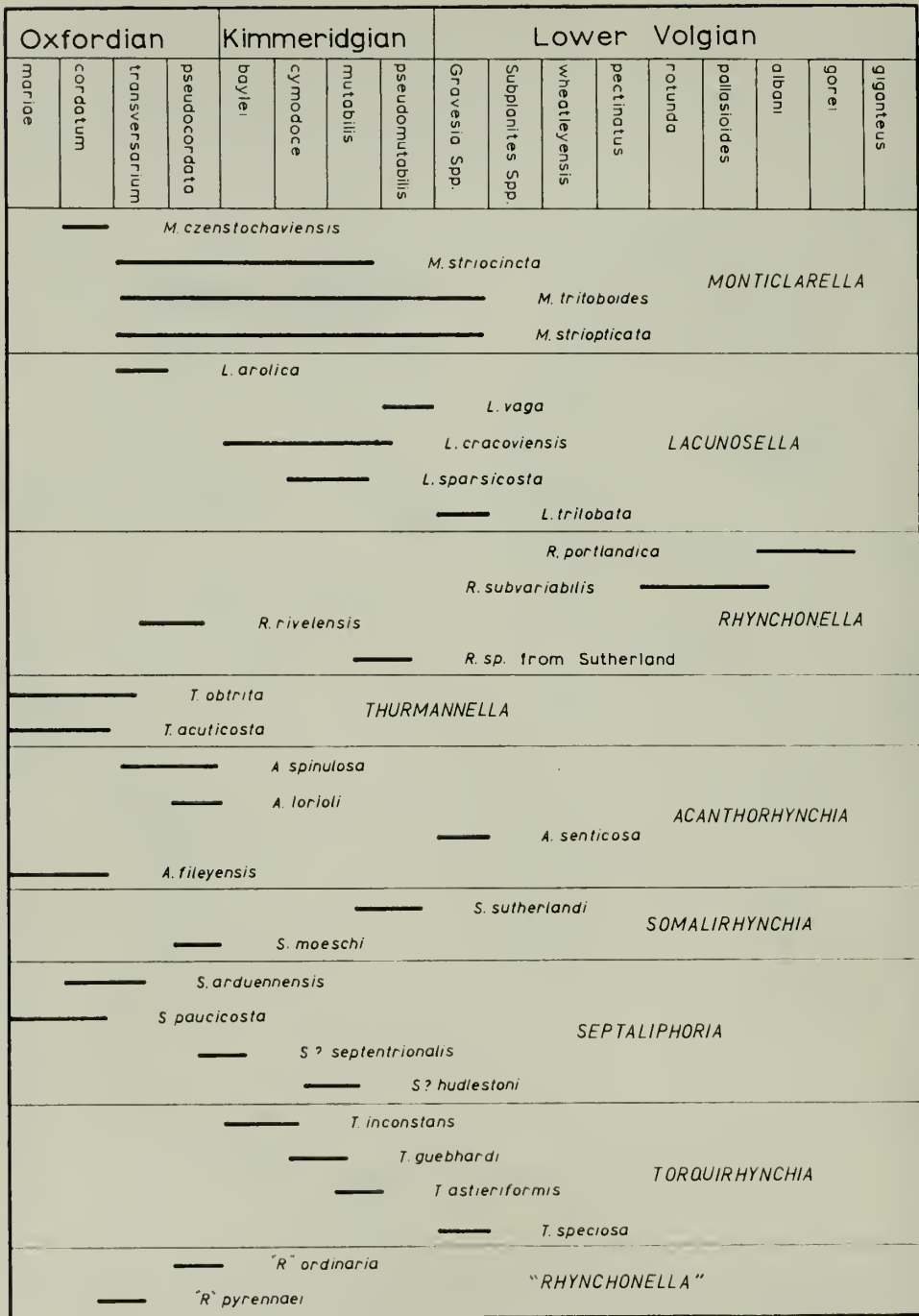


FIG. 6. The stratigraphical ranges of the Upper Jurassic rhyntonellids here described.

In order to help clarify the distribution patterns, text-fig. 2 shows the outcrop of the Upper Jurassic (including the Callovian) and also indicates a generalised palaeogeography of Oxfordian-Kimmeridgian times, after Kuhn (1953). Volgian times saw a major withdrawal of the sea from much of the area and the consequent marked decrease in the rhynchonellid faunas can be seen by comparing text-figs. 4 and 5. This decrease is particularly evident when it is considered that most of the German fauna plotted on text-fig. 5 is probably restricted to the *Gravesia* and *Subplanites* zones of the basal Volgian.

The stratigraphical ranges of the Oxfordian-Volgian species studied are tabulated on text-fig. 6. These ranges have been determined as accurately as possible, but it has often proved difficult to translate records from older stratigraphical papers into modern zonal terms.

MORPHOLOGY

The present author has accepted the definitions of morphological terms used in the "Treatise" (1965) with the exception of the following points :

Within the species studied, it has been found when describing the form of the pedicle opening the choice of term has invariably been limited to either hypothyridid or submesothyridid. In many cases it is extremely difficult to differentiate these types ; in none of the species examined did the pedicle opening strongly impinge on the beak ridges. The second point concerns the pedicle collar ; according to the definition in the "Treatise", this is an internal feature of the ventral beak, "continuous laterally with the internal surface of the deltoidal plates". However, the feature figured by Thomson (1927) under that name consisted of a groove running from the posterior side of the pedicle opening to the tip of the beak. This latter structure has been found in the genus *Acanthothiris* and the term "pedicle trough" is proposed for it.

In describing the internal structures, care has been taken to stress when the features are being described as seen in transverse section and also to avoid misleading descriptions such as "septum long" when in fact it is high. The difficulties present in interpreting transverse sections are further discussed below with reference to the septalium.

The septalium has recently been defined in the "Treatise" as being a "Trough-like structure of the brachial valve between the hinge plates (or homologues), consisting of septalial plates (or homologues), enveloping and buttressed by median septum ; does not carry adductor muscles"; the author would agree with this definition. However, it has been thought necessary to discuss this structure in some detail for two main reasons ; firstly, the author has collected silicified material of *Septaliphoria arduennensis* and *Thurmannella obtrita*, the species in which this structure was originally described by Leidhold (1920), and secondly, because there seems to be some confusion in the literature as to the appearance of the septalium as seen in transverse section.

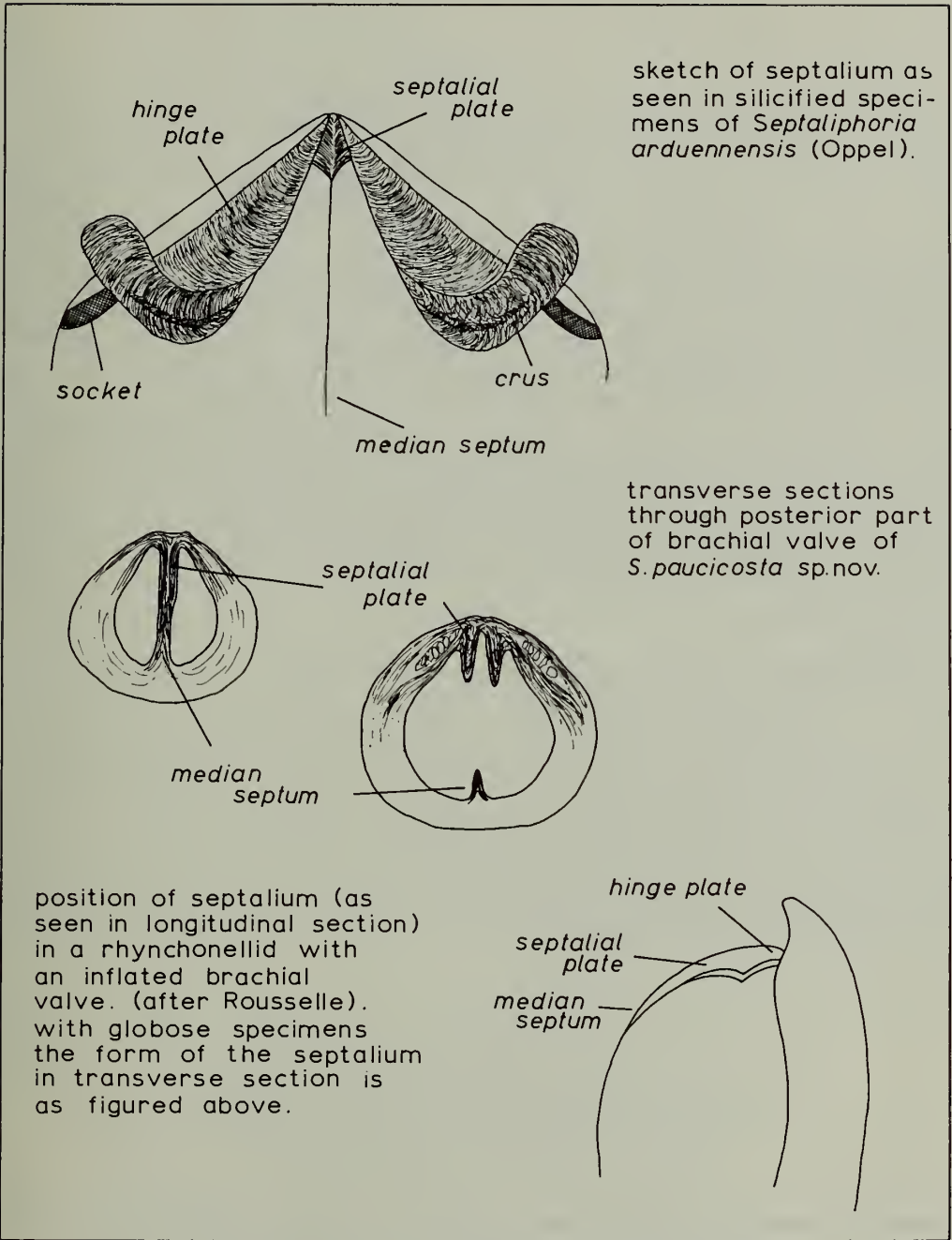
All the elements which together constitute the septalium are capable of considerable variation. This point would seem to be self-evident and yet has undoubtedly

been the cause of some of the misunderstanding. The first full description of the septalium showing its appearance in transverse section was given by Muir-Wood (1934) when she chose as her example the zeilleriid *Digonella digona* (Sowerby), despite the fact that it had originally been defined with reference to a rhyntonellid. The septalium found in *D. digona* is relatively shallow and supported by a high septum. These features, coupled with the flattened nature of the brachial valve, result in the appearance, in transverse section, of a septalium bearing little resemblance to the same structure as seen in most Mesozoic rhyntonellids. As stated above, the septalium in zeilleriids consists of a well developed, shallow trough lying between the hinge plates and supported for some distance by a high median septum. In contrast to this, the septalium in *Septaliphoria arduennensis* is only developed at the extreme posterior end of the valve and is either supported by a very low septum or, as pointed out by Wiśniewska (1932), sometimes appears to rest directly on the floor of the valve. The other point, which was recently discussed by Rousselle (1965), is that the appearance of the septalium in transverse section largely depends on the degree of inflation shown by the brachial valve.

Text-figure 7 shows the septalium developed in *Septaliphoria arduennensis* and also two transverse sections through the posterior part of the brachial valve of *S. paucicosta* sp. nov. These demonstrate the way in which it is possible to have a septalium present and yet not to have the "diagnostic" U-shaped trough in the hinge plates developed in transverse section. From this it is evident that considerable thought should be given to the way in which shell globosity, angle of sectioning and relative development can cause the same structure to show considerable variation in appearance as seen in transverse section. Transverse sections of *S. paucicosta* rather than *S. arduennensis* have been illustrated as the fine detail was better preserved in that species. Rousselle (1965) suggested describing the septalium as either "apparent" or "non apparent" depending on whether or not it appeared "trough shaped" in transverse section. This suggestion does not seem to be particularly useful as a septalium is either present or it is not and its appearance in transverse section is obviously dependent on the factors mentioned above.

The transverse sections of *S. paucicosta* clearly show the way in which the septalial plates are united with the median septum. This latter point has been the subject of some discussion. The figured photomicrograph (pl. 12, fig. 6) of an acetate peel proves conclusively as has been pointed out by several authors (Ager, 1965*b*), that Leidhold (1920) was mistaken in describing the septalium as, "arising from a bifurcation of the dorsal septum at its posterior end and fusion of the forked structures with the hinge plate". The definition in the "Treatise", given above, is obviously the correct interpretation. A photomicrograph of a zeilleriid septalium is figured for comparison with that of *S. paucicosta* on pl. 12.

In the genera described, the author has recognized four of the crural types so far defined namely, radulifer, calcarifer, arcuifer and falcifer. The author would agree with the "Treatise" definitions with the exception of one point concerning the radulifer type. In the material studied, the radulifer crural bases do not arise on the ventral side of the hinge plates but on the dorsal. This is demonstrated by photo-



sketch of septalium as seen in silicified specimens of *Septaliphoria arduennensis* (Opel).

transverse sections through posterior part of brachial valve of *S. paucicosta* sp. nov.

position of septalium (as seen in longitudinal section) in a rhynchonellid with an inflated brachial valve. (after Rousselle). with globose specimens the form of the septalium in transverse section is as figured above.

FIG. 7. Sketches to show the form of the septalium in the genus *Septaliphoria* Leidhold.

micrographs of an acetate peel of the crural bases of *Septaliphoria paucicosta* (pl. 12). In some species with radulifer crura such as *Acanthothiris spinosa*, the crural bases are only poorly differentiated.

Calcarifer type crura have been found in the genera *Thurmannella* and *Ivanoviella*; the form of the crura in these genera was strictly comparable to those observed in a specimen of *Rhynchonelloidella smithi* sectioned for comparison. Although, as pointed out in the "Treatise", distally the calcarifer are similar in form to the falcifer, in mode of occurrence and proximal appearance they differ markedly. Text-figures showing the form of falcifer crura are given with the specific descriptions of *Lacunosella arolica*, *L. sparsicosta*, *L. cracoviensis* and *L. vaga*. The most striking difference is that, by using acetate peels, it can be seen that the early formed parts of the crura lie within the hinge plates of the species with calcarifer crura while in *Lacunosella* the hinge plates are never united and the early formed parts of the crura are external to them and never surrounded by hingeplate material (pl. 12). This feature also differentiates falcifer crura from the radulifer and arcuifer types, apart from considerations of gross morphology. The crural bases are formed by the deflection of hinge plate material around these early formed portions of the crura (pl. 12). Whether or not the crural bases are clearly differentiated depends partly on whether the early crus was rounded or sharply pointed, and also on how closely the hinge plate material followed the original shape. Although the early crus may have been sharply pointed, this shape may be lost completely or reduced to a rounded swelling on the dorsal side of the hinge plates where the latter are much thickened.

Arcuifer crura are only recorded in the genus *Monticlarella*. Three species of that genus were investigated, using acetate peels, but the preservation was poor in all cases and no information additional to that given in the "Treatise" was obtained.

Cardinal processes of the type found in certain Palaeozoic rhynchonellids such as the Uncinulidae are not developed in the material studied and, within the Upper Jurassic, only the genus *Acanthorhynchia* shows any comparable structure. In that genus the inner hinge plates are characteristically thickened and in some species this gives rise to a low rounded process on the ventral side of the hinge plates. A photomicrograph of the thickened hinge plates of *Acanthorhynchia (Acanthorhynchia) panacanathina* is figured on plate 12.

Order RHYNCHONELLIDA Kuhn, 1949

Superfamily RHYNCHONELLACEA Gray, 1848

Family DIMERELLIDAE Buckman, 1918

Subfamily MONTICLARELLINAE nov.

DIAGNOSIS. Small rhynchonellids; ornament includes radial striae; ribs absent or variably developed; beak small and pointed; slightly sulcate, recti-marginate or weakly uniplicate; crura arcuifer where known.

STRATIGRAPHICAL RANGE. Lower Jurassic—basal Cenomanian.

Genus *MONTICLARELLA* Wiśniewska

- 1932 *Monticlarella* Wiśniewska, pp. 55-57.
 1960 *Monticlarella* Wiśniewska; Makridin, p. 248.
 1965b *Monticlarella* Wiśniewska; Ager, p. H604.

TYPE SPECIES. *Rhynchonella czenstochaviensis* Roemer, by original designation.

EMENDED DIAGNOSIS. Small subpentagonal or subtriangular rhynchonellids; radial ornament always includes striae and usually ribs; small, sharp beak; crura arcuifer.

STRATIGRAPHICAL RANGE. Upper Jurassic—? Lower Cretaceous.

DESCRIPTION. *External characters.* All the included species are small, subpentagonal or subtriangular, symmetrical and biconvex. The valves may be of equal convexity or the pedicle valve may be the more inflated. The small, pointed, suberect to erect beak does not obscure the hypothrydid pedicle opening; deltidial plates, when present, are small and disjunct. A small flattened interarea and distinct beak ridges are developed.

One of the most distinctive features is the ornament which always includes radial striae, even though these may be restricted to the troughs between the ribs. Ribs, rounded or subrounded, are usually present, although not on the type species: the variation in the development of the ribbing is a useful criterion for specific differentiation. The anterior commissure is either rectimarginate, uniplicate or slightly sulcate.

Internal characters. None of the specimens sectioned was particularly well preserved.

Pedicle valve. Dental lamellae are present but are usually only weakly developed and invariably only attached, if at all, to the extreme posterior of the valve. The teeth are strong and usually inserted almost vertically into their sockets.

Brachial valve. The median septum, if present, is low; septalial plates are not developed. Inner and outer socket ridges are usually well differentiated.

The crura are of the type distinguished by Wiśniewska as arcuifer. She described them as having wide bases, being concave toward the middle and turning distally toward the ventral valve where they are terminated by "a sort of small crural plate in the shape of a hammer". The author would agree with Wiśniewska that the genus has a distinctive type of crura. The most distinctive feature about them as seen in transverse section would seem to be the way in which, from being initially flattened in the plane of articulation, by the development of vertical elements at their inner ends, they again become flattened but lying at right angles to the plane of articulation and slightly to the ventral side of it.

SPECIES. The following nominal species are attributed to the genus

M. czenstochaviensis (Roemer) (1870, p. 247, pl. xxii, figs. 12-14)

M. lineolata (Phillips) (as figured by Jacob and Fallot 1913, pp. 17-18, pl. i, figs. 9-14).

M. rollieri Wiśniewska (1931, pp. 59-60, pl. vi, figs. 10-11)

M. striocincta (Quenstedt) (1852, p. 455, pl. xxxvi, fig. 24)

M. strioplicata (Quenstedt) (1852, p. 455, pl. xxxvi, fig. 23)

M. triloboides (Quenstedt) (1852, p. 455, pl. xxxvi, fig. 29)

DISTRIBUTION. The genus occurs most commonly in the Swabian and Franconian Jura ; outside those areas it has only definitely been recorded from Poland and the French Jura and in both these regions it is a very scarce form. Makridin (1964) does not record it from the Russian Platform, although it is stated to occur there in the Russian " Treatise ".

OCCURRENCE. The three species investigated in detail all have consistently well developed pedicle openings which, it is reasonable to assume, indicate a functional pedicle in the adult stage. This latter fact, coupled with the wide distribution of the species and the fact that they can occur in a variety of high energy environments, suggests that the mode of life could well have been one of attachment either to sponges or floating material. This hypothesis would account for the diversity of environment in which the genus occurs.

***Monticlarella czenstochaviensis* (Roemer)**

(Pl. I, fig. 4, text-fig. 8)

1870 *Rhynchonella Czenstochaviensis* Roemer: 247-48, pl. 22, figs. 12-14.

1917 *Rhynchonella Czenstochaviensis* Roemer; Rollier: 116.

1932 *Monticlarella czenstochowiensis* (Roemer); Wiśniewska: 57-58, pl. 6, figs. 13-18.

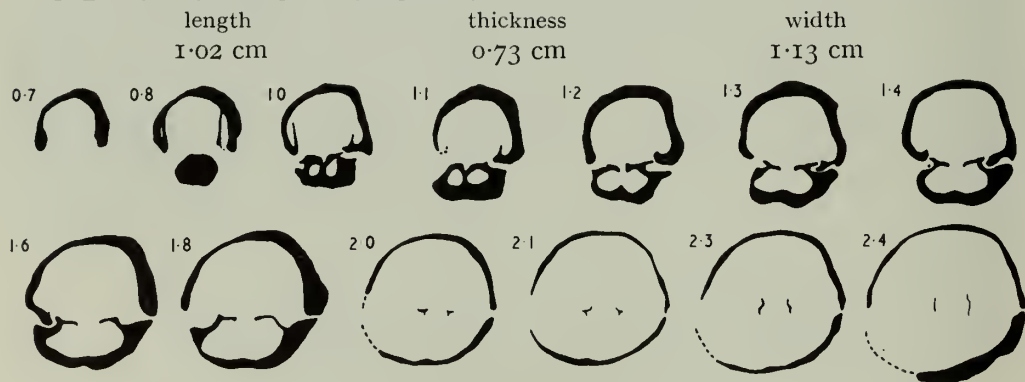
EMENDED DIAGNOSIS. Medium sized, subtriangular *Monticlarella* ; maximum width well toward anterior margin ; valves equally biconvex or with the pedicle valve the more inflated ; rectimarginate ; test covered by fine radial striae ; concentric growth lamellae may be present ; crura arcuifer.

STRATIGRAPHICAL RANGE. Lower Oxfordian—*cordatum* zone.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Roemer (1870) pl. xxii, figs. 12-14, from " Clarenberges " near Czenstochowa, Poland.

MATERIAL. 5 specimens collected by Dr. D. A. B. Pearson from the Holy Cross Mts., Poland. 2 specimens obtained by Dr. D. V. Ager from the type locality.

DIMENSIONS OF FIGURED SPECIMEN.



MONTICLARELLA CZENSTOCHOWIENSIS (Roemer)

Oxfordian, Poland. J.1219/2

FIG. 8. Transverse serial sections of *Monticlarella czenstochaviensis* (Roemer) kindly made available by Dr. D. V. Ager. Numerals represent distance in millimetres from pedicle umbo.

DISTRIBUTION. The species has only been recorded from Poland.

REMARKS. The figured specimen and the series of serial sections were kindly made available by Dr. D. V. Ager. Lack of material precludes a full description but, from the limited material available and the specimens which have been figured, the species appears to be both consistent and distinctive.

Although Wiśniewska (1932) did not give any reason why she changed the name, it is presumed that she did so on grounds of incorrect transliteration. However, as this is not permissible under the International Code of Zoological Nomenclature, Article 32, (a) ii, the author has reverted to the original spelling of Roemer (1870).

Monticlarella striocincta (Quenstedt)

(Pl. 1, figs. 1-3, text-fig. 9)

- 1852 *Terebratula striocincta* Quenstedt: 455, pl. 26, fig. 24.
 1858 *Terebratula striocincta* Quenstedt: 634, pl. 78, fig. 12.
 1871 *Terebratula striocincta* Quenstedt: 131, pl. 40, figs. 17-19.
 1885 *Terebratula striocincta* Quenstedt: 694, pl. 53, fig. 57.
 1886 *Rhynchonella* cf. *striocincta* (Quenstedt); Opper and Waagen: 295.
 1917 *Rhynchonella striocincta* (Quenstedt); Rollier: 119.
 1932 *Monticlarella striocincta* (Quenstedt); Wiśniewska: 58-59, pl. 6, fig. 12.

EMENDED DIAGNOSIS. Small, subpentagonal *Monticlarella*; anterior commissure rectimarginate or slightly sulcate; pedicle valve much more inflated than the brachial; ornament of fine striae passing anteriorly into coarser ribs; crura arcuifer.

STRATIGRAPHICAL RANGE. Oxfordian—Kimmeridgian: *transversarium* to *mutabilis* zones.

TYPE SPECIMEN. Lectotype, here designated, fig. 16, pl. 40 in Quenstedt (1871) from the "Malm gamma" of Lochen, Germany.

MATERIAL. 90 specimens from the collection of the University of Tübingen; 2 specimens collected by the author from the southern French Jura; 1 specimen from the collection of the Geology Department, Imperial College, London.

DESCRIPTION. *External characters.* The shell is biconvex with the pedicle valve the more inflated; this results largely from the distinctive manner in which the posterior part of the pedicle valve bends over so that the top of the very small, pointed beak lies almost at right angles to the lateral commissure. Although the beak lies in this position it is not sufficiently incurved to obscure the delthyrium. In the material studied, the small, disjunct deltidial plates mentioned by Wiśniewska (1932) have not been observed and there is an open delthyrium.

The test ornament is distinctive and consists posteriorly of numerous fine striae which pass anteriorly into well developed, rounded ribs formed by the fusion of several striae; the striae continue in the troughs between the ribs as far as the anterior margin. Growth lamellae are usually present but tend to be sparsely distributed and only poorly developed.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
0.80 cm	0.55 cm	0.75 cm
0.92 cm	0.67 cm	0.83 cm
0.88 cm	0.60 cm	0.86 cm

Internal characters. Pedicle valve. The dental lamellae are very much reduced and not attached to the ventral wall of the shell. The teeth are inserted at a relatively shallow angle, as seen in transverse section.

Brachial valve. There is no median septum. The sockets are shallow and inner and outer socket ridges are scarcely differentiated.

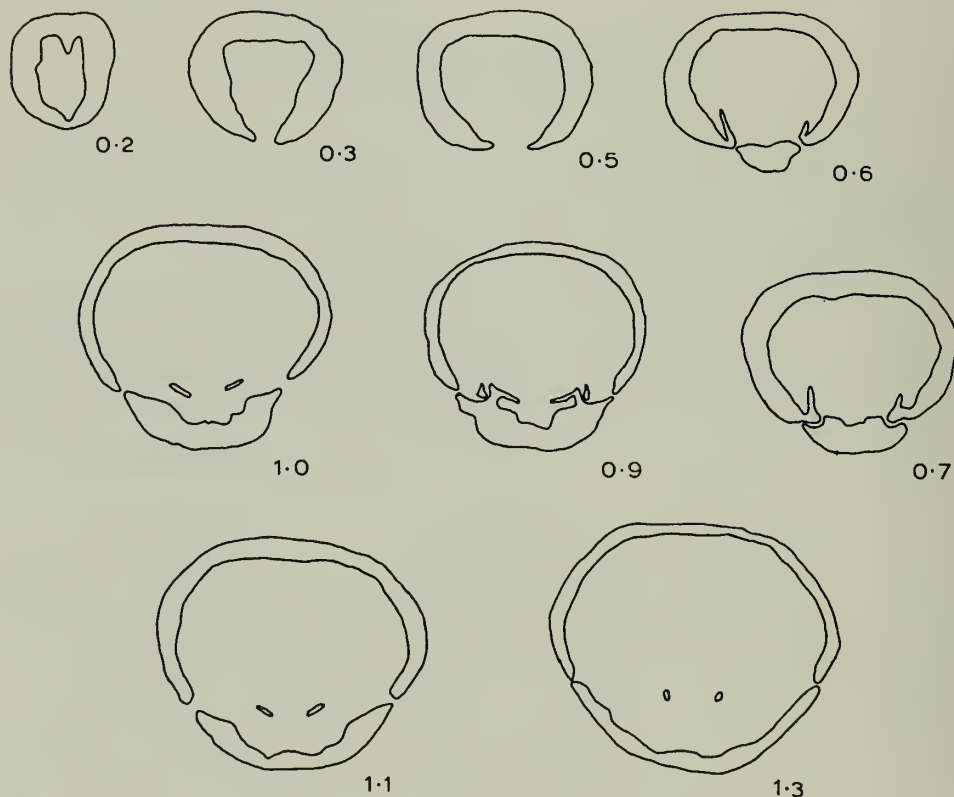


FIG. 9. Transverse serial sections of *Monticlavella striocincta* (Quenstedt). "Weiss Jura alpha". Lochengründe, Germany. Specimen donated by the University of Tübingen. ($\times 8$).

DISTRIBUTION. The Swabian and Franconian Jura, Poland and the southern French Jura are the only areas from which the species has been definitely recorded. It is considered likely that *M. striocincta* could occur quite widely in the French Jura but has been overlooked on account of its small size.

OCURRENCE. Unfortunately Wiśniewska (1932) does not give any details of the associated fauna or of the type of lithology from which her material was obtained and Quenstedt (1852, 1871) only says that it occurs with *Terebratula lacunosa*. However, the author visited the original Quenstedt locality of Lochengründle near Tübingen and collected material from "Malm upper alpha" and "lower beta". Both of these horizons are within the sponge reef facies and consist there of interbedded hard, argillaceous limestones and marls, occurring in units ranging from a few inches to two or three feet in thickness. *M. striocincta*, together with *M. strioplicata*, was found to occur predominantly in the marly units and was associated with a varied fauna of terebratulids, including the ribbed "*pectunculus*" types, echinoid plates and spines, small ammonites and sponges; lacunosellid brachiopods were present but were concentrated in the harder limestone bands.

In the southern French Jura (Ain), the species has been collected from the Bedded Virieu Limestone (Ager & Evamy, 1963) just north of Lac d'Armaille. The Bedded Virieu Limestone is here represented by well bedded calc-lutites with alternations of calcareous shale; as well as *M. striocincta*, there is a rich fauna of lamellibranchs, terebratulids and the large asymmetrical rhynchonellid *Torquirhynchia guebhardi*. *M. striocincta* is one of the least abundant elements of the fauna, the majority of which suggests a high energy environment at or above wave-base (Evamy, 1963 unpublished thesis). *M. striocincta* has also been collected in this area from the argillaceous Chavoley Beds and details of the occurrence are given under *Lacunosella arolica*.

Monticlarella triloboides (Quenstedt)

(Pl. I, figs. 5-7, text-fig. 10)

- 1852 *Terebratula triloboides* Quenstedt: 455, pl. 26, fig. 29.
 1858 *Terebratula triloboides* Quenstedt: 643, pl. 78, fig. 13.
 1871 *Terebratula triloboides* Quenstedt: 129, pl. 40, figs. 6-9.
 1876 *Rhynchonella triloboides* (Quenstedt); Loriol: 188, pl. 23, figs. 41-43.
 1885 *Terebratula triloboides* Quenstedt: 694, pl. 53, fig. 58.
 1904 *Rhynchonella triloboides* (Quenstedt); Loriol: 279, pl. 27, figs. 36-38.
 1913 *Rhynchonella triloboides* (Quenstedt); Jacob and Fallot: 34.
 1917 *Rhynchonella triloboides* (Quenstedt); Rollier: 119.
 1918 *Stolmorhynchia triloboides* (Quenstedt); Buckman: 46.
 1932 *Monticlarella triloboides* (Quenstedt); Wiśniewska: 62-63, pl. 6, figs. 8-9.

EMENDED DIAGNOSIS. Medium to large sized subpentagonal *Monticlarella*; about 15-20 simple ribs; no posterior smooth area; radial striae only present in the troughs between the ribs; uniplication in anterior commissure; crura arcuifer.

STRATIGRAPHICAL RANGE. Oxfordian—Kimmeridgian—Lower Volgian; accurate records range from the *transversarium* to *Gravesia* zones, Quenstedt states that it is most abundant in the "Malm gamma", i.e. *cymodoce* and *mutabilis* zones.

TYPE SPECIMEN. Lectotype, here designated, fig. 8, pl. 40 of Quenstedt (1871) from the "Malm gamma" of Bosler, Germany.

MATERIAL. 320 specimens from the collection of the University of Tübingen; 17 specimens collected by Dr. Enay from near Arinthod (Jura).

DESCRIPTION. *External characters.* The shell is equally biconvex and has a small, pointed, erect beak. The oval pedicle foramen is flanked by disjunct deltidial plates which show a characteristic thickening around the actual opening. Beak ridges and interarea are both well developed.

The ornament consists of about 20 rounded ribs, as counted at the anterior margin, which mostly originate at the umbones although a few also arise by dichotomy. The well marked uniplication in the anterior commissure usually carries about six of these ribs. A distinctive feature of the species is the radial striae which can be seen only in the troughs between the ribs of well preserved specimens; these striae are usually most easily observable toward the anterior margin. The better preserved specimens also show a concentric ornament of very fine growth lines, which are usually more apparent posteriorly; growth lamellae are rarely developed.

The shell of many of the broken and worn specimens is seen to be of a very fibrous character; whether this is its original condition or the result of post-burial recrystallisation, as evidenced by the loss of the fine detail, is not known. Although the shell fibres and the radial striae superficially resemble one another, the striae may be differentiated by the fact that they are more individually distinct and occur only in the troughs, whereas the fibres appear as a compact mass and may be visible on any part of the shell. If the top layer of the shell has been removed so that the fibrous condition is visible, this inevitably means that the striae will have been obliterated.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.00 cm	0.68 cm	1.00 cm
0.87 cm	0.59 cm	0.87 cm
1.27 cm	0.84 cm	1.26 cm

Internal characters. Pedicle valve. The shell is quite thick and the dental lamellae are relatively well developed. The teeth are inserted vertically into the sockets, as seen in transverse section.

Brachial valve. There is no median septum or ridge developed; other details are as in generic description.

DISTRIBUTION. The species is known from the Swabian and Franconian Jura, Poland and the central French Jura. The only other record is that of Jacob and Fallot (1913) from the "Portlandien supérieur" of Chomérac (Ardèche).

OCCURRENCE. The author has not collected the species and it is only briefly recorded in the literature. Quenstedt (1871) noted that it occurred with *Terebratula lacunosa*. The horizon cited by Jacob and Fallot appears to yield a very varied rhynchonellid fauna, some of which is almost certainly referable to the genus *Lacunosella* Wiśniewska. The material of Dr. Enay came from a fine grained marl from which specimens of *Acanthorhynchia* (*Echinirhynchia*) *lorioli* were also obtained.

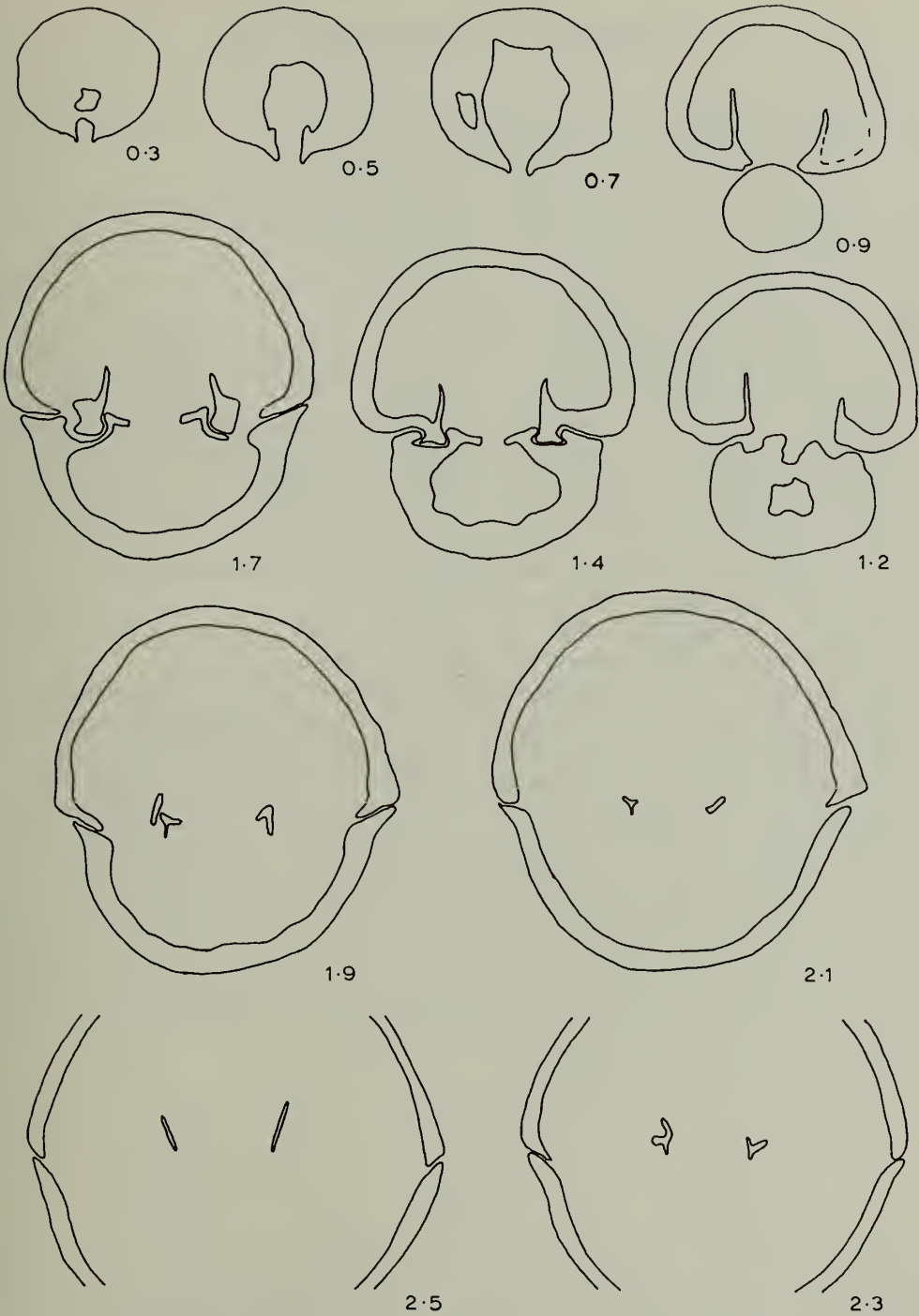


FIG. 10. Transverse serial sections of *Monticlarella triloboides* (Quenstedt). "Malm gamma", Germany. Specimen donated by the University of Tübingen. ($\times 8$).

Monticlarella strioplicata (Quenstedt)

(Pl. I, figs. 8-10, text-fig. 11)

- 1852 *Terebratula strioplicata* Quenstedt: 455, pl. 26, fig. 23.
 1858 *Terebratula strioplicata* Quenstedt: 635, pl. 78, fig. 24.
 1871 *Terebratula strioplicata* Quenstedt: 132, pl. 40, figs. 24-32.
 1885 *Terebratula strioplicata* Quenstedt: 694, pl. 53, fig. 59.
 1909 *Rhynchonella strioplicata* (Quenstedt); Simionescu: 40, 41, 94, pl. 7, fig. 18.
 1913 *Rhynchonella strioplicata* (Quenstedt); Jacob and Fallot: 17.
 1917 *Rhynchonella strioplicata* (Quenstedt); Rollier: 123.
 1917 *Rhynchonella strioplanata* (Quenstedt); Rollier: 123.
 1917 *Rhynchonella pauciplicata* Rollier: 123.
 1917 *Rhynchonella tenuiplicata* Rollier: 123.
 1917 *Rhynchonella furcatella* Rollier: 123.
 1932 *Monticlarella strioplicata* (Quenstedt); Wiśniewska: 60-62, pl. 6, figs. 1-7, text-fig. 18.

EMENDED DIAGNOSIS. Medium sized, subpentagonal to slightly elongate *Monticlarella*; rectimarginate or with a low uniplication; ornament of fine striae posteriorly passing anteriorly into short coarse ribs; crura arcuifer.

STRATIGRAPHICAL RANGE. Oxfordian—Kimmeridgian—Lower Volgian; *transversarium* to *Gravesia* zones.

TYPE SPECIMEN. Lectotype, here designated, fig. 25, pl. 40 of Quenstedt (1871) from the "Malm gamma" of Lochen, Germany.

MATERIAL. 11 specimens from the collection of the University of Tübingen; 22 collected by the author from Swabia and Franconia.

DESCRIPTION. *External characters.* The shell is biconvex with the pedicle valve slightly more inflated than the brachial. The beak is small, sharply pointed and erect. The oval, hypothyriddid pedicle opening is small and is flanked by two small, discrete deltidial plates. Beak ridges and interarea are only poorly developed.

Posteriorly the ornament consists of very fine striae, while on the anterior half or third of the shell are developed five or six relatively coarse ribs. The fine striae continue to the anterior of the shell only in the troughs between the ribs. The outline varies from subpentagonal to suboval, specimens having the former shape being wider and having more ribs; the length is usually greater than the width. There appears to be a complete gradation between the two forms at all stratigraphical levels for which there is material available; however, the material is relatively limited and it is not possible to say whether the proportions of the two forms change or have any stratigraphical value.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.18 cm	0.80 cm	1.13 cm
1.04 cm	0.68 cm	0.98 cm
1.05 cm	0.70 cm	0.78 cm

Internal characters. Pedicle valve. Dental lamellae are present but only poorly developed and attached to the shell wall only at their posterior extremities. The teeth are strong.

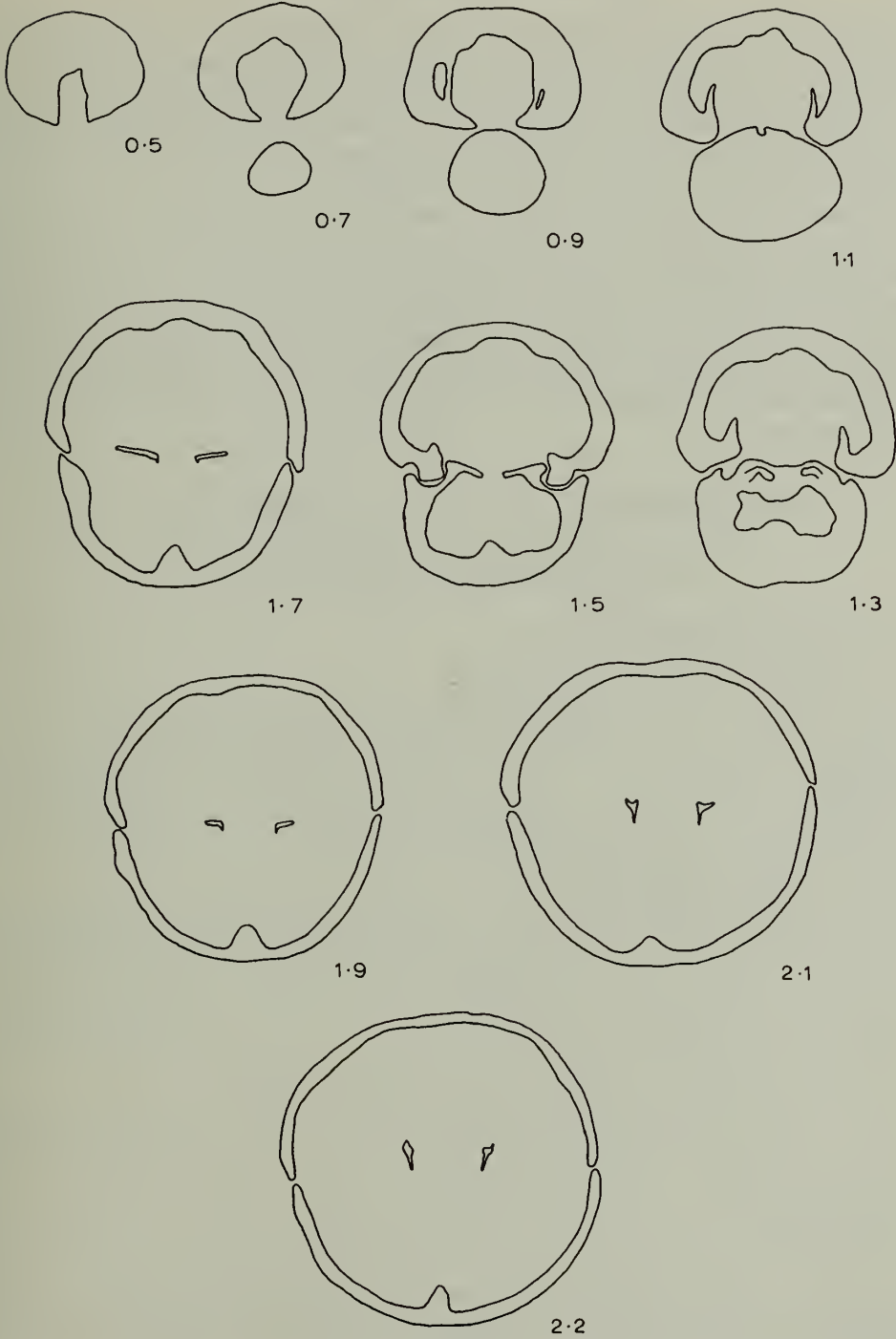


FIG. 11. Transverse serial sections of *Monticlavella strioplicata* (Quenstedt). "Malm gamma". Barrenberg, Germany. ($\times 8$).

Brachial valve. A long, well developed median ridge is present. The hinge plates are flat. Both the inner and outer socket ridges are clearly differentiated.

DISTRIBUTION. Apart from the Swabian and Franconian Jura and Poland, the only other records of the species are those of Jacob and Fallot (1913) from Mont Crussol and from Chomérac (Ardèche). A possible specimen of *M. strioplicata* was figured by Struckman (1878) from near Hanover.

OCCURRENCE. The species has been collected by the author from only two localities, namely, at Lochengründle in the Swabian Jura and at Barrenberg in Franconia. The former locality has been described in the remarks on the occurrence of *M. striocincta*. The latter locality is of "Malm gamma" age and is again in the sponge reef facies. The fauna included many lacunosellids, terebratulids, small sponges, ammonites and occasional belemnites and echinoids, with *M. strioplicata* one of the least abundant faunal elements. This locality is further described under *Lacunosella sparsicosta*.

Family **WELLERELLIDAE** Likarev in Rzhonsnitskaya, 1956

Subfamily **LACUNOSELLINAE** Smirnova, 1963

Genus **LACUNOSELLA** Wiśniewska, 1932

1932 *Lacunosella* Wiśniewska: 30-32.

1960 *Lacunosella* Wiśniewska; Makridin: 254.

1965 *Lacunosella* Wiśniewska; Ager: 608.

TYPE SPECIES. *Rhynchonella arolica* Oppel, by original designation.

EMENDED DIAGNOSIS. Medium to large rhynchonellids; outline usually sub-pentagonal; ribs bifurcate; beak small; beak ridges and interarea poorly developed; shell massive; very reduced dental lamellae; crura falcifer.

STRATIGRAPHICAL RANGE. Oxfordian—Kimmeridgian—Lower Volgian; upper *cordatum* to *Gravesia* spp. zones.

DESCRIPTION. *External characters.* The shell is either equally biconvex or with the brachial valve the more inflated. The test frequently has a characteristic and distinctive translucent, pearly appearance. Although the outline is usually sub-pentagonal, it may be strongly trilobate as in *L. trilobata*. The genus is usually symmetrically developed with a uniplication in the anterior commissure, however, this feature is frequently displaced by asymmetrical development and completely asymmetrical, bilobed variants are produced by *L. trilobata*.

The ribbing is variable and in different species the rib count at the anterior commissure varies between five and twenty-five. One of the most distinctive external features is that while not all the ribs bifurcate, this character is invariably shown by some of them.

A small suberect beak is present, as are beak ridges and an interarea although both the latter are only poorly developed. The submesothyridid pedicle opening is flanked by conjunct deltidial plates. Concentric ornament, which is neither strongly developed nor consistently present, comprises fine growth lines and weakly developed growth lamellae.

Internal characters. Pedicle valve. The most striking features are the massive shell and the very reduced dental lamellae ; lateral cavities are hardly developed. Pedicle collars were not present in all the species sectioned but as it seems probable that these are only developed in the adult specimens, their absence may be the result of sectioning slightly immature material. The teeth are strong and frequently show some degree of crenulation ; lateral denticulae are usually present. In fully adult specimens the muscle attachment areas can be clearly seen as quite deep depressions in the shell.

Brachial valve. There is no septalium and the median septum, if present, is very much reduced. The hinge plates are divided and, almost as soon as the cavity of the brachial valve is exposed during serial sectioning, the long falcifer crura can be seen hanging down from them into the brachial valve. The presence of falcifer crura distinguishes *Lacunosella* from all other Upper Jurassic genera. Inner and outer socket ridges are both well-developed.

SPECIES. The following nominal species are attributed to the genus :

- L. amstettensis* (Fraas) (1858, pp. 107-8)
- L. arolica* (Oppel) (1865, p. 312)
- L. blanowicensis* Wiśniewska (1932, pp. 40-1, pl. iii, figs. 1-5)
- L. cracoviensis* (Quenstedt) (1871, p. 136, pl. xl, fig. 43)
- L. dilatata* (Rollier) (1917, p. 134)
- L. kozłowski* Wiśniewska, (1932, pp. 54-55, pl. v, figs. 1-7)
- L. monsalvensis* (Gilliéron) (1873, p. 244, pl. x, figs. 11-12)
- L. multiplicata* (Zieten) (1832, p. 55, pl. xli, fig. 5)
- L. polita* (Quenstedt) (1871, p. 126, pl. xxxix, fig. 106)
- L. prosimilis* (Rollier) (1917, p. 174)
- L. pseudodecorata* (Rollier) (1917, p. 139)
- L. selliformis* (Lewiński) (1908, p. 437, pl. xxii, fig. 8-11)
- L. silicea* (Quenstedt) (1871, p. 129, pl. xxxix, fig. 107)
- L. siemiradzki* (Wiśniewska) (1932, pp. 48-49, pl. iii, figs. 21, 22)
- L. sparsicosta* (Quenstedt) (1858, pp. 633-34, pl. lxxviii, figs. 12-22)
- L. subsimilis* (Schlotheim) (1820, p. 264)
- L. trilobata* (Zieten) (1832, p. 56, pl. xlii, fig. 3)
- L. trilobataeformis* Wiśniewska (1932, pp. 46-48, pl. iv, figs. 1-11)
- L. vaga* sp. nov.
- L. visulica* (Oppel) (1866, p. 295).

DISTRIBUTION. The genus has been recorded throughout the French, German and Swiss Jura, from Poland and from Stramberk, Czechoslovakia.

OCCURRENCE. With the exception of the occurrence of *L. vaga* on the Col du Chat (Savoie) the genus is always associated with sponges. This association has been commented on by Quenstedt (1871), Ager and Evamy (1963) and Ager (1965a). The genus is most abundant and varied in the Swabian and Franconian Jura where it occurs in the bedded limestones associated with the sponge reefs.

The massive shell and consistent presence of a pedicle opening, presumably indicating a functional pedicle, seem to be adaptations to a high energy environment

around the reefs. The persistent occurrence of sponges with *Lacunosella* is so striking that it suggests that the genus was in some way dependent on them. Several times while collecting material, the author found specimens of *Lacunosella* actually in contact with sponges. While this may have been coincidence, it could also have been the result of the rhynchonellids actually having been attached to the sponges. It is difficult to see what particular benefit this would have been and why *Lacunosella* should have restricted itself to attachment on that particular 'host'. At the locality mentioned above where sponges are not present, *L. vaga* was obtained from bedded limestones associated with "reef" limestones.

***Lacunosella arolica* (Oppel)**
(Pl. I, figs. 11-12, text-figs. 12-13)

- 1864 *Rhynchonella lacunosa* (Schlotheim); Heer: 137, fig. 87.
 1865 *Rhynchonella Arolica* Oppel: 312.
 1866 *Rhynchonella Arolica* Oppel; Oppel and Waagen: 294.
 1867 *Rhynchonella Arolica* Oppel; Moesch: 310-311, pl. 7, fig. 9.
 1871 *Terebratula lacunosa Arolica* Quenstedt; 127, pl. 39, figs. 95-96.
 1885 *Terebratula lacunosa Arolica* Quenstedt: 693, pl. 53, fig. 60.
 1890 *Rhynchonella lacunosa* (Quenstedt) var. *Arolica* Oppel; Haas: 48-50, pl. 3, figs. 1-22, pl. 4, figs. 1-5.
 1917 *Rhynchonella Arolica* Oppel; Rollier: 134.
 1918 *Stolmorhynchia arolica* (Oppel); Buckman: 46.
 1932 *Lacunosella arolica* (Oppel); Wiśniewska: 33-38, pl. 2, figs. 1-18.

EMENDED DIAGNOSIS. Medium to large sized, relatively flattened *Lacunosella*; outline subpentagonal; 9-11 low, subangular ribs; crura falcifer.

STRATIGRAPHICAL RANGE. Oxfordian—upper *cordatum* and *transversarium* zones.

TYPE SPECIMEN. In his original description of the species Oppel cited the figure in Heer (1864) listed above.

MATERIAL. 16 specimens collected by the author from the southern French Jura in the British Museum (Nat. Hist.) nos. BB. 45630-45639, BB. 45678-45681; 43 specimens collected by Dr. Enay from the central French Jura; 12 specimens from the "Birmensdorfer-Schichten" of Switzerland donated by the Naturhistorisches Museum, Basel.

DESCRIPTION. *External characters.* The shell is biconvex with the brachial valve slightly the more inflated; however, both valves are relatively flattened compared with other species of the genus. The beak is small and suberect; beak ridges and interarea are hardly differentiated. The small, submesothyridid pedicle opening is flanked by conjunct deltidial plates.

The radial ornament consists of about eleven low, subangular ribs, the majority of which originate at the umbones although bifurcation is not uncommon. Numerous fine growth lamellae are characteristically present. The anterior commissure has a well-marked uniplication which usually carries three or four ribs; however, it is often distorted to some degree by asymmetrical development.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3.30 cm	2.35 cm	3.78 cm
2.86 cm	2.20 cm	3.22 cm

Internal characters. The internal characters have been investigated using material collected near Virieu-le-Grand (Ain) in the southern French Jura. Although not topotypic, the material is of the correct age and is not far from Trept (Isère), a locality mentioned by Oppel (1866) in his original description of the species.

Pedicle valve. A well developed pedicle collar is present in adult specimens. The shell is massive and while lateral cavities are present they are of a very reduced nature and bounded by slender dental lamellae. Although the dental lamellae are very slight, the teeth are strongly supported by the thick shell wall.

Brachial valve. There is a low median septum ; other characters as in generic description.

DISTRIBUTION. The species appears to occur quite abundantly throughout the French and Swiss Jura and in Poland. That *L. arolica* has not been recorded from either the Swabian or Franconian Jura is attributed to the fact that the "Sponge reef" facies did not develop in that area until the lower Kimmeridgian.

OCCURRENCE. The material collected by the author came from the Chavoley Beds (Ager & Evamy, 1963) near Virieu-le-Grand (Ain). These beds, consisting of calcareous marls and shales, represent the only argillaceous interruption in the succession of carbonate sediments which constitute the Upper Jurassic of the southern French Jura. The associated fauna included hexactinellid sponges and rare specimens of *Monticlavella striocincta*. *L. arolica* was the commonest element in the fauna and is also abundant in the "Birmensdorfer Schichten" of the type area in Switzerland.

***Lacunosella vaga* sp. n.**

(Pl. 2, figs. 1-3, text-fig. 14)

1932 ?*Septaliphoria pinguis* (Roemer); Wiśniewska: pl. 1, figs. 13, 14, NON figs. 1-11, 15-20.

NAME. Latin *vagus*-a-um : wandering, the species has a wide geographical distribution.

DIAGNOSIS. Medium-sized, symmetrical, sub-pentagonal *Lacunosella* ; beak small ; 16-20 subangular ribs ; no posterior smooth area ; crura falcifer.

STRATIGRAPHICAL RANGE. Kimmeridgian—only accurately recorded from the upper *mutabilis* and lower *pseudomutabilis* zones.

TYPE SPECIMEN. Holotype, no. BB. 44135, obtained from *mutabilis* zone at Sermérieu (Isère), France.

DIMENSIONS OF HOLOTYPE. Length 2.69 cm, thickness 2.00 cm, width 3.02 cm.

MATERIAL. 43 specimens from type locality ; 22 specimens Col du Chat (Savoie) ; 28 specimens from Franconia. All except the figured specimens are in the author's collection, British Museum (Nat. Hist.) nos. BB. 45668-73, BB. 45756-61.

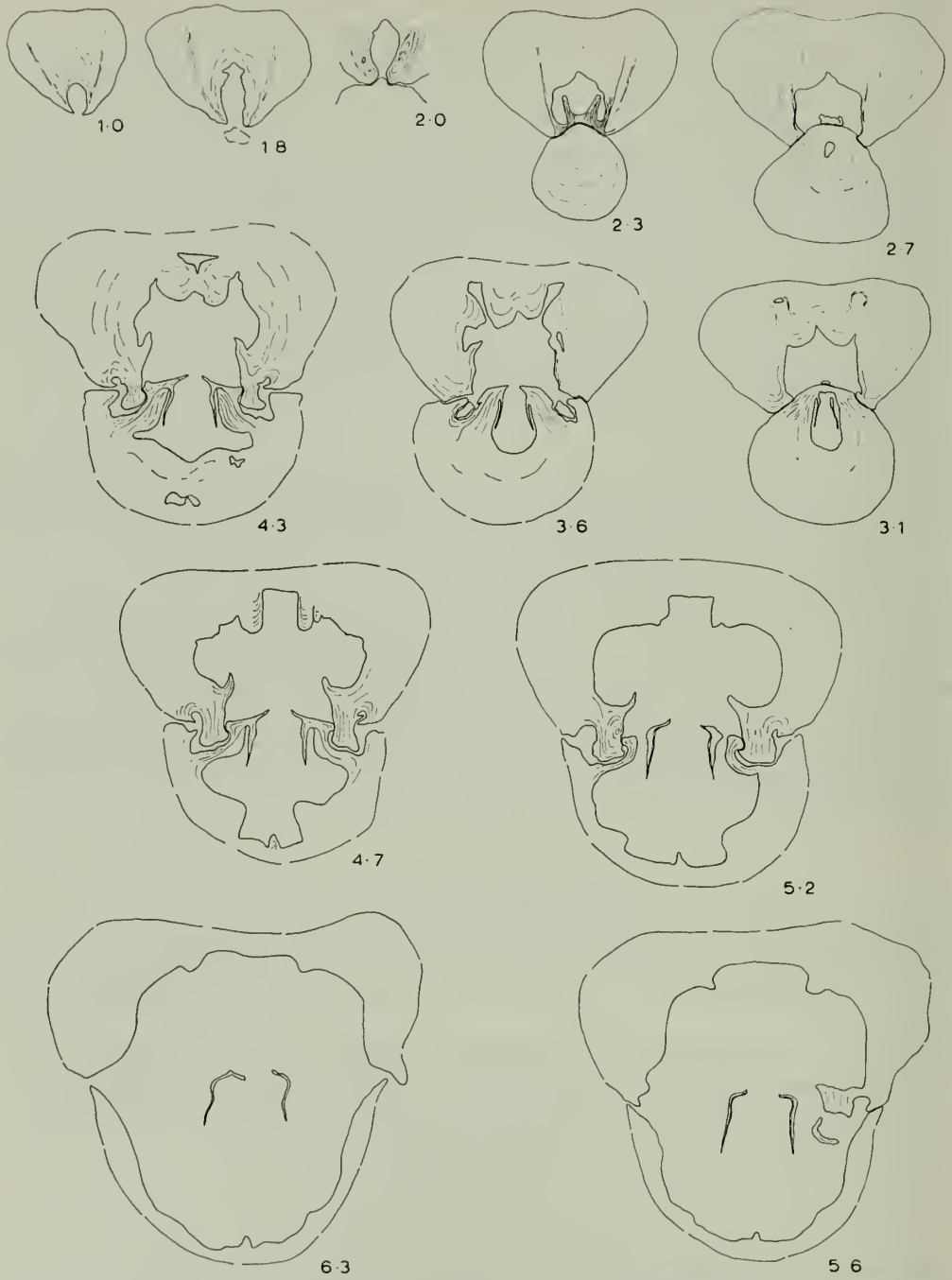


FIG. 12. Transverse serial sections of *Lacunosella arolica* (Oppel). Oxfordian. Chavoley Beds. Virieu-le-Grand (Ain), France. ($\times 3$).

DESCRIPTION. *External characters.* *L. vaga* is weakly trilobate with a low, symmetrical uniplication in the anterior commissure. The brachial is the more inflated valve and the species is generally characterised by a rather globose appearance. Concentric ornament is only rarely present and consists of weak growth lamellae and numerous fine growth lines. The beak is typically small and sub-erect; conjunct deltidial plates delimit the small submesothyridid pedicle opening. Beak ridges and an interarea are present but only poorly developed.

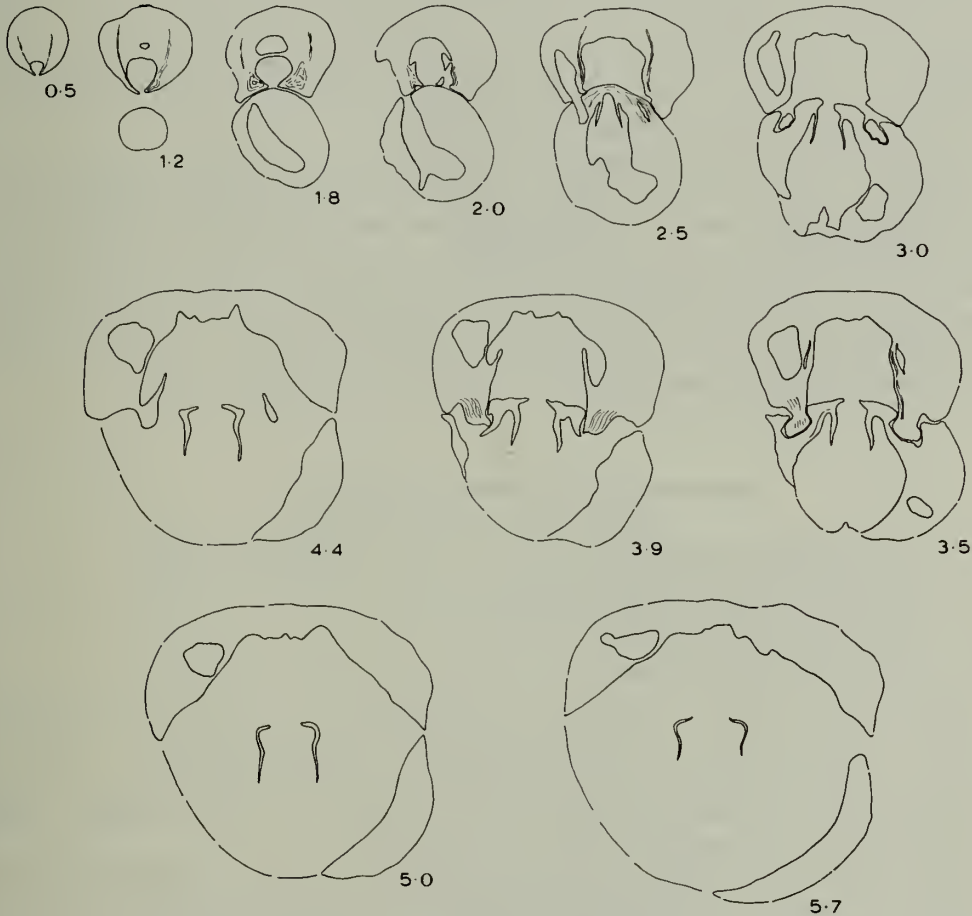


FIG. 13. Transverse serial sections of *Lacunosella arolica* (Oppel). Oxfordian. Chavoley Beds. Virieu-le-Grand (Ain), France. ($\times 3$).

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.69 cm	2.00 cm	3.02 cm
2.84 cm	1.84 cm	3.06 cm
2.78 cm	1.90 cm	2.97 cm

Internal characters. Pedicle valve. Shell massive and the muscle impressions deeply inserted. The teeth are strongly developed and lateral denticulae are present.

Brachial valve. Typical lacunosellid falcifer crura are developed. Very strong inner and outer socket ridges are present.

DISTRIBUTION. The species has been collected by the author from the southern French Jura in the Départments of Savoie and Isère and from the Franconian Jura. Two of the specimens from Poland figured by Wiśniewska (v. synonymy) as *Septaliphoria pinguis* are externally identical with *L. vaga* and, as they also come from the same horizon, it seems very likely that Wiśniewska misattributed them. This suggestion is borne out by the fact that Róyzicki (1948) recorded *S. pinguis* sensu Wiśniewska from sponge reefs. If this is the case, then the geographical distribution of the species would be considerably extended.

OCCURRENCE. At the type locality, *L. vaga* is associated with *Torquirhynchia* cf. *astieriformis* and details of the locality are given under that species. The specimens collected from the Col du Chat (Savoie) were from fine-grained, bioclastic limestones. This record is interesting in that it is the only occurrence of *Lacunosella* known to the author where the genus is not associated with sponges; many of the specimens were crushed and the only other fossils collected from the locality were terebratulids. The Franconian material was found with the typical association of sponges, ammonites, terebratulids and lamellibranchs at the base of a small reef.

***Lacunosella cracoviensis* (Quenstedt)**
(Pl. 2, figs. 5–6, text-fig. 15)

- 1871 *Terebratula trilobata cracoviensis* Quenstedt: 136, pl. 40, fig. 43.
 1871 *Terebratula lacunosa subsimilis* (Schlotheim); Quenstedt: 129, pl. 39, fig. 78.
 1917 ?*Rhynchonella cracoviensis* (Uhlig); Rollier: 172.
 1917 *Rhynchonella prosimilis* Rollier: 174.
 1932 *Lacunosella cracoviensis* (Quenstedt); Wiśniewska: 41–46, pl. 2, figs. 6–20.

EMENDED DIAGNOSIS. Medium-sized, subpentagonal *Lacunosella*; prominent narrow, suberect beak; 17–25 fine, bifurcating ribs; crura falcifer.

STRATIGRAPHICAL RANGE. Upper Oxfordian—Lower Kimmeridgian; in Swabia and Franconia it has been recorded from the “beta” and “gamma Malm” while Wiśniewska gives its range in Poland as “Sequanien”.

TYPE SPECIMEN. Lectotype, here selected, fig. 43, pl. 60 in Quenstedt (1871), from the “Coralrag” of Przegorzaty, Poland.

MATERIAL. 7 specimens, collection of Tübingen University from Swabia; 21 specimens, author’s collection from Franconia and Swabia, in the British Museum (Nat. Hist.) nos. BB. 45650–67, BB. 45674–77.

DESCRIPTION. *External characters.* *L. cracoviensis* is a medium-sized *Lacunosella*; although the outline is subpentagonal, it shows considerable variation and either length or width may be the greater dimension.

The subangular ribs are relatively fine, commence at the umbones and are often bifurcate. The anterior commissure is usually symmetrical with a low uniplication

developed but not uncommonly it shows varying degrees of asymmetry. There are usually 8-9 ribs on the fold.

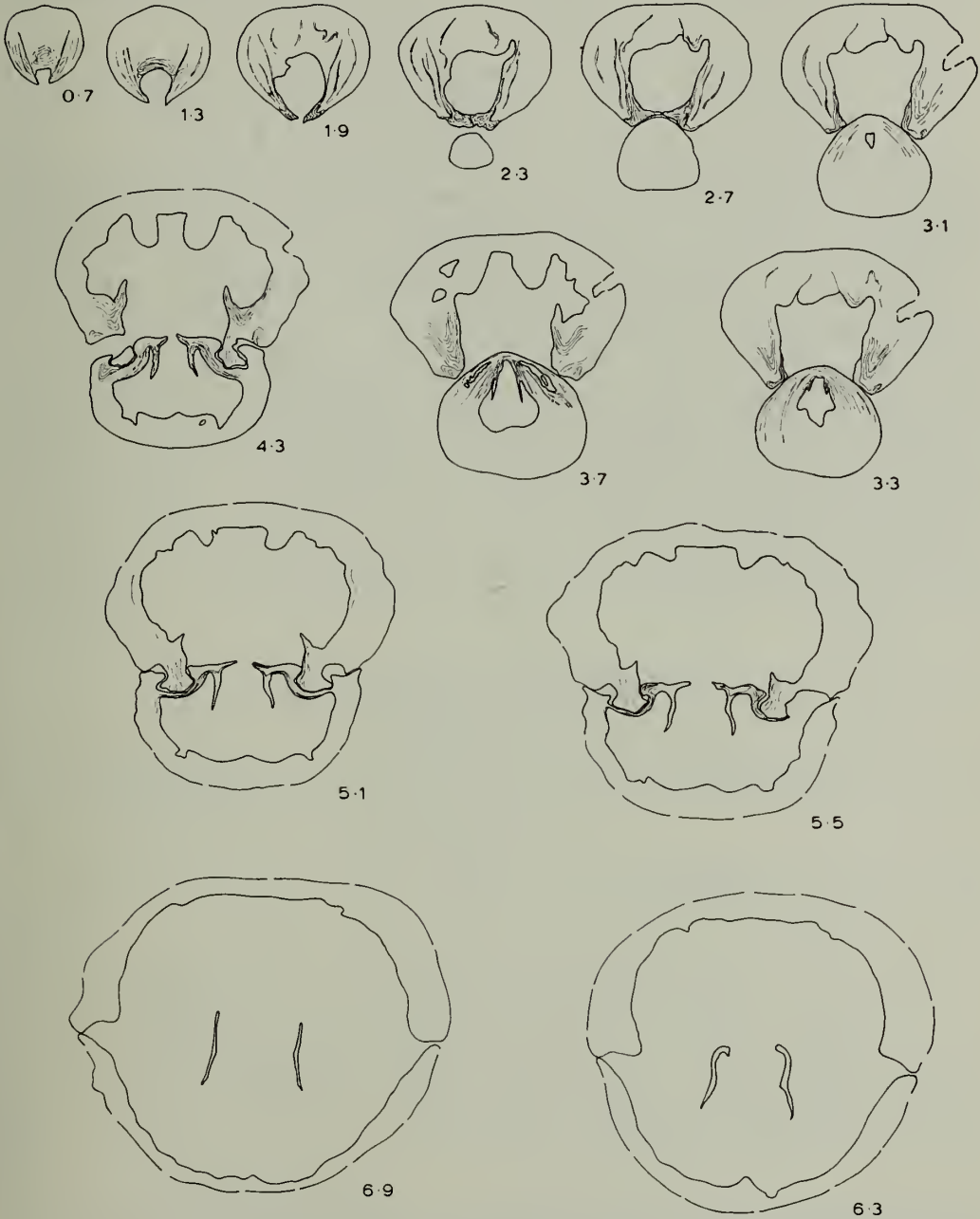


FIG. 14. Transverse serial sections of *Lacunosella vaga* sp. nov. Topotype. Kimmeridgian—*mutabilis* zone. Sermérieu (Isère), France. ($\times 3$).

The suberect beak is narrow and characteristically pronounced. The interarea and beak ridges are scarcely developed. The submesothyridid pedicle opening is small and flanked by conjunct deltidial plates.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.62 cm	1.40 cm	2.50 cm
2.76 cm	1.97 cm	2.94 cm

Internal characters. Pedicle valve. The shell is massive; lateral cavities are not developed as the dental lamellae do not appear to touch the ventral shell wall. A pedicle collar is present. The teeth are strongly developed and lateral denticulae are present.

Brachial valve. The falcifer crura are exceptionally wide distally. Inner and outer socket ridges are very strongly developed.

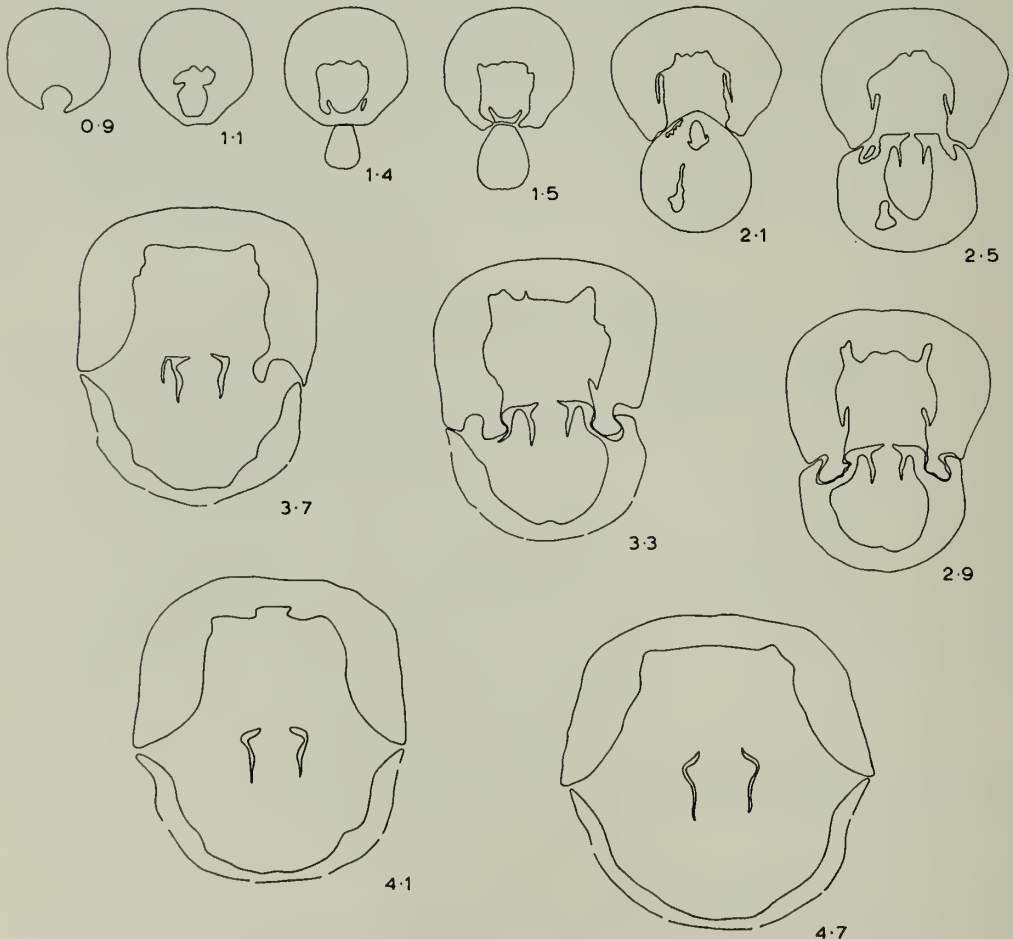


FIG. 15. Transverse serial sections of *Lacunosella cracoviensis* (Quenstedt). "Malm beta/gamma". Würgau, Germany. ($\times 4$).

DISTRIBUTION. The species is recorded from Poland, and the Swabian and Franconian Jura.

OCCURRENCE. Occurs in association with sponge reefs, together with the usual fauna of ammonites and terebratulids.

REMARKS. The name *cracoviensis* was first used by Quenstedt (1871) in describing material from the area of Krakow, Poland; the specimen he then figured, pl. 60, fig. 43, has been selected as lectotype. The species has been well figured by Wiśniewska (1932) and the author would agree with her in placing in synonymy the specimen figured by Quenstedt (1871), pl. 39, fig. 78, as *Terebratula lacunosa subsimilis* from the "Malm beta". This latter specimen undoubtedly belongs to this rather variable species and other German material from this horizon can be matched exactly with the specimens figured by Wiśniewska from Poland.

The name *subsimilis* was coined by Schlotheim (1820) for material from the "Hornstein", near Amberg, which is generally assumed to be "Malm epsilon" in age. Quenstedt figured a specimen of *subsimilis* of this age (pl. 39, fig. 108). Rollier (1917) proposed the name *prosimilis* for the specimen figured by Quenstedt from the "Malm beta" in order to differentiate it from *subsimilis* of Schlotheim. No specimens from the "Malm epsilon" referable to the Schlotheim species have been examined. It has been decided, in view of the stratigraphic diastem, namely "Malm upper gamma" and "delta" which separates it from *L. cracoviensis*, together with the fact that lack of material makes taxonomic revision impossible, to continue to regard *subsimilis* as a separate species restricted to the "Malm epsilon".

Lacunosella sparsicosta (Quenstedt)

(Pl. 2, figs. 7-8, text-fig. 16)

1858 *Terebratula lacunosa sparsicosta* Quenstedt: 633-34, pl. 78, figs. 19-22.

1871 *Terebratula lacunosa sparsicosta* Quenstedt: 126-28, pl. 39, figs. 92-93, ?94.

1890 *Rhynchonella lacunosa* var. *sparsicosta* (Quenstedt); Haas: 51-52, pl. 6, figs. 9-12, 15-17.

1917 *Rhynchonella sparsicosta* (Quenstedt); Rollier: 140.

EMENDED DIAGNOSIS. Small to medium-sized, subpentagonal *Lacunosella*; 6-7 ribs anteriorly of which 2-3 lie on the fold; posterior smooth area present; crura falcifer.

STRATIGRAPHICAL RANGE. It appears to be restricted to the "Malm gamma", which is equivalent to the *cymodoce* zone of the Kimmeridgian.

TYPE SPECIMEN. Lectotype, here selected, fig. 93, pl. 39 in Quenstedt (1871), from the "Malm gamma" of Käsbühl, Germany.

MATERIAL. 10 specimens, author's collection from Franconia in British Museum (Nat. Hist.) nos. BB. 45640-49. 35 specimens, collection of Tübingen University from Swabia; 13 specimens, collection of the Naturhistorisches Museum, Basel, from the Schaffhausen area.

DESCRIPTION. *External characters.* *L. sparsicosta* is one of the smallest species in the genus; it is subpentagonal in outline and has a strong uniplication in the anterior commissure. It is biconvex with the brachial valve considerably more

inflated than the pedicle. The most frequent number of ribs developed is seven, of which three lie in the fold; these latter ribs are coarse and subangular, contrasting with the lower more rounded ones occurring laterally. There is a posterior smooth area, as the ribs do not originate from the umbones; the central ribs are, however, developed much further posteriorly than the lateral ones. The ribs are mostly simple. Growth lamellae are usually present but are very variably developed.

The beak is small and suberect. A small, submesothyridid pedicle opening is flanked by small, conjunct deltidial plates. The interarea and beak ridges are only very poorly differentiated.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.61 cm	1.03 cm	1.73 cm
1.98 cm	1.93 cm	2.23 cm

Internal characters. Pedicle valve. There is a well-developed pedicle collar. The shell is massive and the dental lamellae are only poorly developed so that lateral cavities are hardly present. The delthyrial cavity is subquadrate and ventrally the depressions of the muscle attachment areas can be clearly seen. The teeth are strong and lateral denticulae are present.

Brachial valve. Inner and outer socket ridges are both well-developed. Other features are as described for the genus.

DISTRIBUTION. The species ranges from the northern Franconian Jura through the Swabian Jura to the Schaffhausen area of Switzerland.

OCCURRENCE. The author has only collected the species from one locality, namely Barrenberg in Franconia. The exposure there was not very good but appeared to represent perireefal limestones which had been broken up and the resulting angular blocks recemented. *L. sparsicosta* was the commonest element in a rich fauna which also included sponges, ammonites, *L. cracoviensis*, *Monticlavella striplicata* 'normal' terebratulids and the sulcate terebratulid *Nucleolata*.

Lacunosella trilobata (Zieten)

(Pl. 3, figs. 3-6)

- 1832 *Terebratula trilobata* Münster; Zieten: 56, pl. 42, fig. 3.
 1832 *Terebratula inaequilatera* Goldfuss; Zieten: 56, pl. 42, fig. 4.
 1845 *Terebratula trilobata* Zysner: pl. 5, figs. 1-5.
 1870 *Rhynchonella trilobata* Moesch: 145, pl. 14, fig. 33.
 1871 *Terebratula trilobata* Quenstedt: 134-36, pl. 40, figs. 35-39, ?figs. 40-44.
 1890 *Rhynchonella trilobata* (Zieten); Haas: 55-58, pl. 7, figs. 3-6.
 1917 *Rhynchonella trilobata* (Zieten); Rollier: 175.
 1917 *Rhynchonella inaequilatera* (Zieten); Rollier: 176.
 1918 *Stolmorhynchia trilobata* (Zieten); Buckman: 46.
 1932 *Lacunosella trilobata* (Zieten); Wiśniewska: 32.

EMENDED DIAGNOSIS. Medium-sized, elongated *Lacunosella*; very strongly trilobate or asymmetrical; 17-24 rather shallow, subangular ribs of which 6-9 lie on the fold.

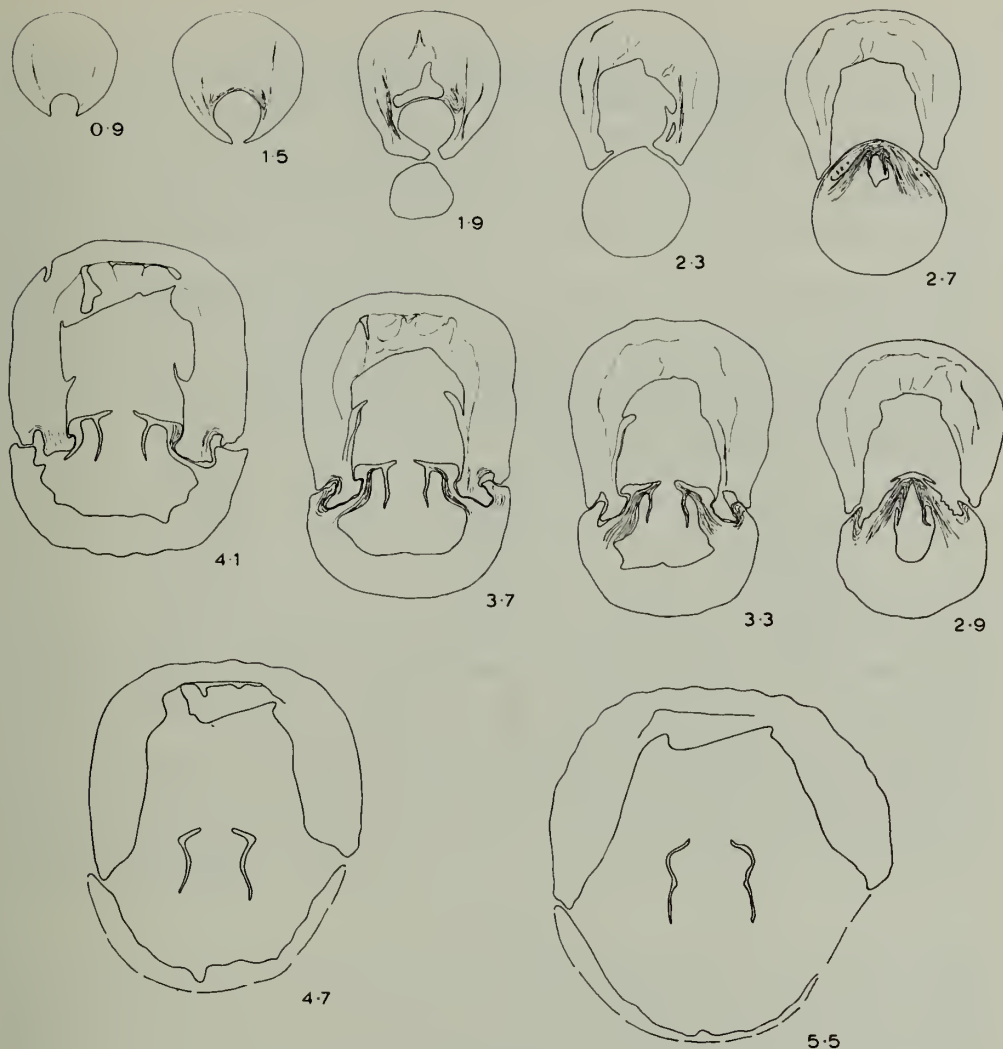


FIG. 16. Transverse serial sections of *Lacunoseella sparsicosta* (Quenstedt). "Malm gamma". Barrenberg, Germany. ($\times 4$).

STRATIGRAPHICAL RANGE. The species has only been recorded from the "Malm epsilon" i.e. Lower Volgian.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Zieten, pl. 42, fig. 3. Although Zieten attributes the species to Münster, the reason for this is not known as there does not appear to be any publication of Münster's prior to Zieten in which the species is mentioned. Sherborn (1930) throws no light on the matter, attributing *speciosa* to "von Münster in Zieten". Similarly, there seems no reason for his attribution of *Terebratulina inaequilatera* to Goldfuss.

MATERIAL. 2 specimens from the collection of the University of Tübingen; 1 specimen from the collection of the Naturhistorisches Museum, Basel, coming from

the "Kimmeridgien of Württemberg"; 5 specimens in author's collection from the "Malm epsilon" of Franconia, in the British Museum (Nat. Hist.) nos. BB. 45750-54.

DESCRIPTION. *External characters.* The most striking feature of the species is the very marked trilobation shown by most specimens. The species appears to be unique, at least in the upper Jurassic, in that it shows a complete gradation of forms between trilobate symmetrical and bilobed strongly asymmetrical forms. Especially in the trilobate specimens, the brachial valve tends to be considerably the more inflated.

The bifurcating ribs vary considerably in number and development; generally their coarseness is inversely proportional to the number present. The concentric ornament, when present, consists of numerous fine growth lines. The beak is small and flanked by weakly developed beak-ridges; the interarea is slightly incurved. The small pedicle opening is limited by conjunct deltidial plates.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3.06 cm	2.25 cm	2.80 cm
2.85 cm	2.05 cm	3.19 cm
2.85 cm	1.63 cm	2.78 cm
3.46 cm	2.55 cm	3.21 cm

Internal characters. These were not investigated as the author's collection contains only a very limited number of sufficiently well preserved specimens.

DISTRIBUTION. The species appears to be restricted to the Swabian and Franconian Jura and the Schaffhausen area of Switzerland.

OCCURRENCE. The specimens collected by the author were obtained from well-bedded, fine-grained limestones; they were the most abundant element in a fauna which also included ammonites and sponges. The fact that so few complete specimens were obtained is a result of the extremely hard, brittle nature of the host rock.

***Lacunosella* sp.**

Specimens have been selected from material in the collection of the University of Tübingen in order to conform as nearly as possible to the specimens figured by Quenstedt (1858, 1871) as *Terebratula lacunosa multiplicata* (pl. 3, fig. 1) and *T. lacunosa decorata* (= *Rhynchonella pseudodecorata* of Rollier) (pl. 1, fig. 13). The author has not personally collected material referable to this species and as there is only a very limited amount available at Tübingen, it has not been possible to give full descriptions. "*Rhynchonella*" *pseudodecorata* is of particular interest as it has been selected by Makridin (1955) as the type of his genus *Isjuminelina* (= *Isjuminella*). As this species seems to be externally a typical member of *Lacunosella*, it is considered that Makridin probably misidentified his material as his description of its internal structures excludes it from that genus.

Also figured is a specimen of *L. selliformis* (Lewiński) (pl. 2, fig. 4) from the Oxfordian of Poland and a specimen of *L. trilobataeformis* Wiśniewska (pl. 3, fig. 2). The latter is strongly homoeomorphic with *Somalirhynchia moeschi* and these two species appear to have been frequently confused in the past.

Family **RHYNCHONELLIDAE** Gray, 1848
 Subfamily **RHYNCHONELLINAE** Gray, 1848
 Genus **RHYNCHONELLA** Fischer, 1809

- 1809 *Rhynchonella* Fischer: 35.
 1918 *Rhynchonella* Fischer: Buckman, 57.
 1920 *Eurhynchonella* Leidhold: 352.
 1932 *Rhynchonella* Fischer; Wiśniewska: 13.
 1957 *Rhynchonella* Fischer; Ager: 1-15.
 1960 *Rhynchonella* Fischer, Makridin: 252.
 1964 *Rhynchonella* Fischer; Makridin: 111-13.
 1965b *Rhynchonella* Fischer; Ager: H610.

REMARKS. It is not proposed to revise the generic description as the type species, *R. loxiae*, does not occur in western Europe and within this area the genus is only represented by rare and very variable "species". *R. loxiae* has recently been described and figured by Ager (1957) and Makridin (1964).

In Britain, there are only two described Jurassic "species" and very little material which can be referred to *Rhynchonella* s.s. The two species are *R. portlandica* Blake and *R. subvariabilis* Davidson; the type of the former was collected from the Lower Portland Sand of "Black Ven" Portland, and of the latter from the Kimmeridge Clay of Potterne, Wilts. Most of the material referable to *Rhynchonella* has been obtained from the "*Rhynchonella* Marls" and various horizons in the Portland Sand exposed on the Dorset coast. Apart from this, there are two specimens from the Lydite Bed of Long Crendon, Buckinghamshire, and six specimens from the Kimmeridgian Boulder Beds of Sutherland. Material from these horizons is very scarce and the author is indebted to the curators of the Geological Museum, Oxford, the Sedgewick Museum, Cambridge, and the B.M.(N.H.), for allowing him to use the specimens in their collections.

An interesting series of specimens collected by Prof. M. R. House from the Upper Blackmore Beds, Portland, is figured on plate 4. As these were collected from the same horizon and locality, it can be reasonably assumed that they represent a single variable species. The variation ranges, however, between end-members, which, if they occurred separately and without intermediate forms, would undoubtedly be referred to *R. portlandica* and *R. subvariabilis*. This suggests that perhaps all the British material from this area should be referred to a single species. However, it is considered that further stratigraphically accurately located material is needed before the full range and variation can be determined; until then it seems pointless to try and define taxonomic groups within this plexus of forms which is at present represented by less than thirty specimens, of which few are complete. It is interesting to note that Blake (1880) in proposing his species *R. portlandica*, commented, "One can scarcely feel quite certain whether this is a distinct species from *R. subvariabilis*".

Specimens were collected by the author from the Boulder Beds of Sutherland, and appear to be the first record of the genus from that area. Again, as with the material from the Dorset coast, it does not seem helpful to propose further taxa until more specimens are available.

Makridin (1964) figured several species and subspecies of *Rhynchonella* and a table giving the stratigraphical ranges of these is given below (text-fig. 17); the strati-

BRITISH SPECIES	<i>R. portlandica</i>	<i>R. subvariabilis</i>	<i>R. micropteryx</i>	<i>R. saropaulensis</i>	<i>R. loxiae</i>	<i>R. concentro-spirata</i>	<i>R. vorobievensis</i>	<i>R. rouillieri ellanica</i>	<i>R. rouillieri ujanovski</i>	<i>R. rouillieri rouillieri</i>	RUSSIAN SPECIES
pectinotus											pseudoscythca
rotundo											
pollosioides											panderi
olboni											virgotus
gorei											rosonovi
gigonteus											nikitini
											fulgens
											subditus
											nodiger
											njosonensis
											stenompholo

FIG. 17. The stratigraphical ranges of the Russian and British species of *Rhynchonella* s.s. Details of the Russian species are taken from Makridin (1964).

graphical range of the British *Rhynchonellas* s.s. is also indicated. Some of the forms figured by Makridin from the Russian Platform seem to be quite close to British specimens although the variation of the genus was such that none of the forms from these two areas is considered to be conspecific.

The most distinctive British element seems to be the form with a long, posterior smooth stage and strong, short ribs anteriorly. This form is represented in the specimens collected by Prof. M. R. House, mentioned above, and is the basis on which such species as *R. riveleensis* and *R. triplicosa* are included in the genus. These species are all characterized by the above features and seem to comprise a persistent stock which is first seen in the basal Callovian and continues to the Volgian. It appears that the form represented by *loxiae* and *portlandica* is restricted to the Volgian.

Rhynchonella riveleensis Loriol

(Pl. 5, figs. 3-6, text-fig. 18)

1904 *Rhynchonella riveleensis* Loriol: 282-83, pl. 26, fig. 43.

EMENDED DIAGNOSIS. Small to medium sized *Rhynchonella*; subpentagonal in outline; slightly incurved interarea; large smooth area posteriorly about 10 strong, subrounded ribs anteriorly; crura radulifer.

STRATIGRAPHICAL RANGE. Oxfordian—upper *transversarium* and lower *pseudocordata* zones.

TYPE SPECIMEN. Lectotype, here selected, fig. 43, pl. 27 of Loriol (1904), the specimen came from the "Argovien II" of Mont Rivel, France.

MATERIAL. 60 specimens from Alex near Oyonnax (Ain); 2 specimens from Choux du Dombief (Jura). All the material was collected by Dr. Enay and subsequently donated to the author.

DESCRIPTION. *External characters.* *R. riveleensis* is subpentagonal in outline and is either equally biconvex or with the brachial valve the more inflated. There is a low uniplication in the anterior commissure and a low fold on the brachial valve. A linguiform extension is only poorly developed. The coarse, simple ribs are only developed on the anterior half to one third of the shell; concentric ornament consists of growth lamellae, most clearly seen on the posterior smooth area, and very fine growth lines.

The beak is small, suberect and sharply pointed. Beak ridges are present and limit the incurved interarea. The deltidial plates project slightly around the hypothyriddid pedicle opening.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.16 cm	0.66 cm	1.22 cm
1.17 cm	0.77 cm	1.25 cm

Internal characters. *Pedicle valve.* The quadrate delthyrial cavity is bounded by long subparallel dental lamellae; the lateral cavities are well developed. The teeth are strong but lateral denticulae are scarcely differentiated.

Brachial valve. There is a long, low median septum; septalial plates are not developed. Inner and outer socket ridges are both present. The clearly marked crural bases are sharply pointed; the radulifer crura become expanded distally.

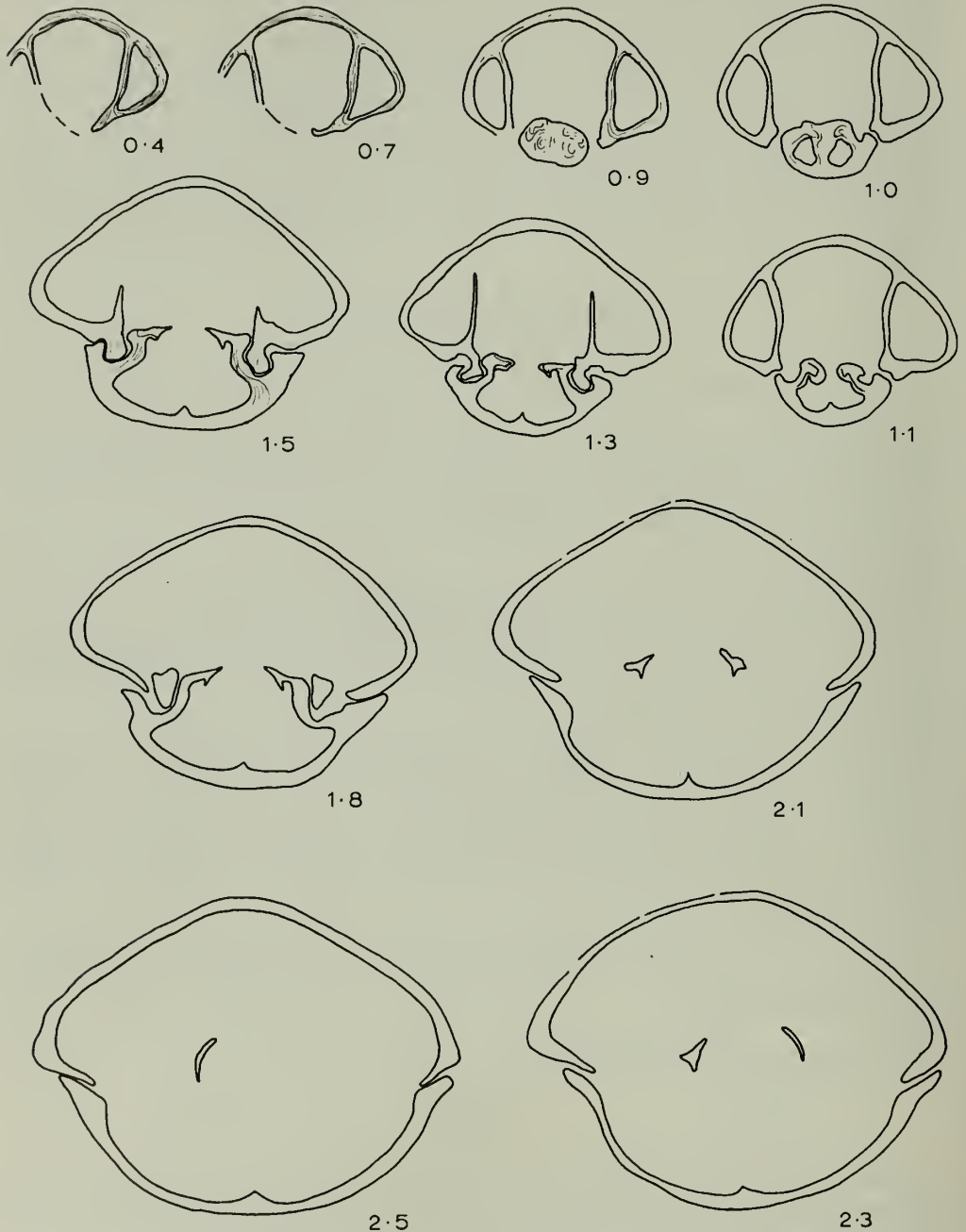


FIG. 18. Transverse serial sections of *Rhynchonella riveiensis* Loriol. Oxfordian—*transversarium* zone. Alex près Oyannax (Ain), France. ($\times 8$).

DISTRIBUTION. The only records of the species are from the central French Jura (Jura lédonien).

OCCURRENCE. Nothing is known except that the material supplied by Dr. Enay came from a pale coloured marl, as evidenced by the adhering matrix.

***Rhynchonella* sp.**

(Pl. 5, figs. 1-2)

REMARKS. The species has not been named or described as only four specimens are known ; these were donated to the author by Dr. D. A. B. Pearson from the Callovian of Kozlowagora in Poland.

Subfamily **IVANOVIPELLINAE** Makridin, 1964

EMENDED DIAGNOSIS. Small to medium sized rhynchonellids ; strong, sub-angular to rounded ribs ; posterior smooth area ; well marked uniplication and linguiform extension often well developed ; septalium present ; crura calcarifer.

STRATIGRAPHICAL RANGE. ?Pliensbachian—middle Oxfordian.

Genus **THURMANNELLA** Leidhold

1920 *Septaliphoria* (*Thurmannella*) Leidhold, pp. 357-62.

1964 *Thurmannella* Leidhold ; Makridin, pp. 143-44.

1965b *Thurmannella* Leidhold ; Ager, pp. 609-10.

TYPE SPECIES. The nominal type species is *Terebratula Thurmanni* Voltz which was designated by Makridin. However, this is regarded by the author as a synonym of *Terebratula obtrita* Defrance and is discussed under the latter species.

EMENDED DIAGNOSIS. Small to medium sized, subpentagonal, rhynchonellids ; ventral valve flattened while the brachial is strongly inflated ; 15-22 simple, sub-rounded to subangular ribs which do not arise at the umbones so that there is a characteristic but variably developed smooth area posteriorly ; well developed uniplication ; linguiform extension usually present but variably developed ; beak small, suberect and sharp ; pedicle opening present ; crura calcarifer.

STRATIGRAPHICAL RANGE. Oxfordian—*mariae* to lower *transversarium* zones.

SPECIES. *T. acuticosta* sp. nov.

T. obtrita (Defrance) (1828, pp. 161-62).

DISTRIBUTION. *Thurmannella* has been recorded from northern France, the northern French Jura, the area around Basel and from Yorkshire and Kent. It is not recorded from Germany.

REMARKS. A diagnosis only has been given as a full description is given of the type species, *T. obtrita* ; and a generic description would only differ in being broadened to include *T. acuticosta*, which differs from *T. obtrita* in having a very limited posterior smooth area, more angular ribs and a more strongly developed uniplication in the anterior commissure.

Thurmannella was first established by Leidhold (1920) as a new subgenus within his new genus *Septaliphoria*. The close relationship thus suggested for *Septaliphoria* and *Thurmannella* is based on their both possessing a septalium. It would appear

that *Thurmannella* was not officially elevated to generic rank until Makridin did so in 1964; it is also described as a genus in the Anglo-American "Treatise" and the author would certainly agree with its separation from *Septaliphoria*.

***Thurmannella obtrita* (Defrance)**

(Pl. 5, figs. 7-9, text-fig. 19)

- 1828 *Terebratula obtrita* Defrance: 161-62.
 1833 *Terebratula Thurmanni* Voltz; Thirria: 172, 179.
 1842 *Terebratula Thurmanni* Voltz; Boyé: 17, pl. 2, fig. 17.
 1859 *Terebratula Thurmanni* Voltz; Opperl: 608.
 1861 *Terebratula Thurmanni* Etallon: 291, pl. 13, fig. 6.
 1865 *Terebratula Thurmanni* Ogérien: 656, 661, text-figs. 294-296.
 1871 *Terebratula Thurmanni* Voltz; Quenstedt: 90-91, pl. 38, figs. 83-87.
 1882 *Rhynchonella Thurmanni* (Voltz); Haas and Petri: 238-240, pl. 7, figs. 14-17.
 1884 *Rhynchonella obtrita* (Defrance); Deslongchamps: 337, pl. 38, figs. 1-3.
 1889 *Rhynchonella obtrita* (Defrance); Haas: 12-13.
 1897 *Rhynchonella Thurmanni* (Voltz); Loriol: 143-46.
 1900 *Rhynchonella Thurmanni* (Voltz); Loriol: 135, pl. 6, fig. 53.
 1901 *Rhynchonella Thurmanni* (Voltz); Loriol: 112, pl. 6, figs. 17-19.
 1904 *Rhynchonella Thurmanni* (Voltz); Loriol: 283.
 1917 *Rhynchonella Thurmanni* (Voltz); Rollier: 154-56.
 1917 *Rhynchonella silicola* Rollier: 155-56.
 1918 *Rhynchonelloidea thurmanni* (Voltz); Buckman: 38.
 1920 *Septaliphoria* (*Thurmannella*) *Thurmanni* (Voltz); Leidhold: 363-65, pl. 5, fig. 6, pl. 6, figs. 10-18.
 1920 *Septaliphoria* (*Thurmannella*) *obtrita* (Defrance); Leidhold: 362-65, pl. 5, fig. 5, pl. 6, figs. 1-9.
 1964 ?*Thurmannella thurmanni* (Voltz); Makridin: 135, pl. 6, fig. 53.

EMENDED DIAGNOSIS. As for genus, except that *T. obtrita* always has a well developed smooth area posteriorly.

STRATIGRAPHICAL RANGE. Lower Oxfordian—*mariae* to lower *transversarium* zones.

TYPE SPECIMEN. In view of the great confusion in the literature, it has been decided that it is necessary to erect a neotype in order to fix the species. The specimen proposed was obtained from the "Terrain à Chailles" of Pagny-sur-Meuse (Meurthe et Moselle). This is the horizon and area of Defrance's original specimens. The specimen is in British Museum (Nat. Hist.) no. BB. 44145.

DIMENSIONS OF NEOTYPE. Length 1.40 cm, thickness 1.35 cm, width 1.72 cm.

MATERIAL. 30 specimens from the "Terrain à Chailles", Pagny-sur-Meuse; in British Museum (Nat. Hist.) nos. BB. 45720-749. 8 specimens from the "Terrain à Chailles", Liesdorf, near Basel; 100 from the *Renggeri* Marl of Arc-sur-Montenot; 18 specimens from the *Renggeri* Marl of Epeugney; 30 specimens from the "ferruginous oolite" of the Verdun area.

DESCRIPTION. *External characters.* The smallest specimens are equally bi-convex, have a laterally suboval outline and only a very low uniplication. All these features become considerably modified with growth and in adult specimens the brachial valve is very much the more inflated and generally the uniplication is very

strongly developed ; is it accompanied by the development of a low fold on the brachial valve. However, the development of the uniplication is very variable and it may be low and rounded even in large specimens. The outline of adult specimens is subpentagonal.

The beak is suberect in the young specimens but becomes characteristically erect in the adult ; it is always relatively small and sharply pointed. At all stages the species possesses a well developed, submesothyridid pedicle opening. The beak is flanked by sharp beak ridges which clearly delimit an incurved interarea. The deltidial plates may be either conjunct or disjunct.

The 15-20 ribs, which are only present on the anterior half to a third of the shell, are low and sub-rounded to sub-angular. The ribs appear to be consistently more rounded on the material from the "Terrain à Chailles"; however, this may, at least in part, be a result of the different preservation. At the extreme anterior of the largest specimens, the ribs sometimes develop a weak trough along their crests.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.42 cm	1.17 cm	1.53 cm
1.73 cm	1.70 cm	1.93 cm
1.40 cm	1.35 cm	1.72 cm

Internal characters. The specimen sectioned was largely silicified with a consequent loss of much fine detail internally.

Pedicle valve. The subquadrate delthyrial cavity is flanked by strong subparallel dental lamellae, which persist, as seen in transverse section, until the teeth have been completely inserted in their sockets. The teeth do not appear to be crenulated ; lateral denticulae are not developed.

Brachial valve. A septalium is present, although, judging from the sectioned specimen and from the silicified material treated with acid, both the median septum and the septalial plates vary considerably in their development. However, some of this apparent variation is almost certainly a result of the incomplete silicification.

Crural bases are well developed ; inner and outer socket ridges are both present. The crura appear to conform in general appearance with the "calcarifer" type described by Muir-Wood (1936). Distally the crura are blade-like and falciform, as can be seen in text-figure 19, however, at their posterior ends they are bent inwards, at almost right angles to their distal ends, to form a "flange". These "flanges" are undoubtedly the structures Leidhold (1920) figured and described as "Cruralspitze". This feature differentiates the crura from the true falcifer type as developed in *Lacunosella*, and it seems that it is the diagnostic feature of calcarifer crura as defined by Muir-Wood (1936). In her original description Muir-Wood described calcarifer crura as consisting "of two flattened, curved, posteriorly concave laminae which project from the hinge plate into the cavity of the dorsal valve. These laminae each unite with a second curved lamina which appears to be suspended from it and projects dorsally like a spur. A ventral extension of this second lamina terminates in a hook-shaped process, the apex of which is directed medianly".

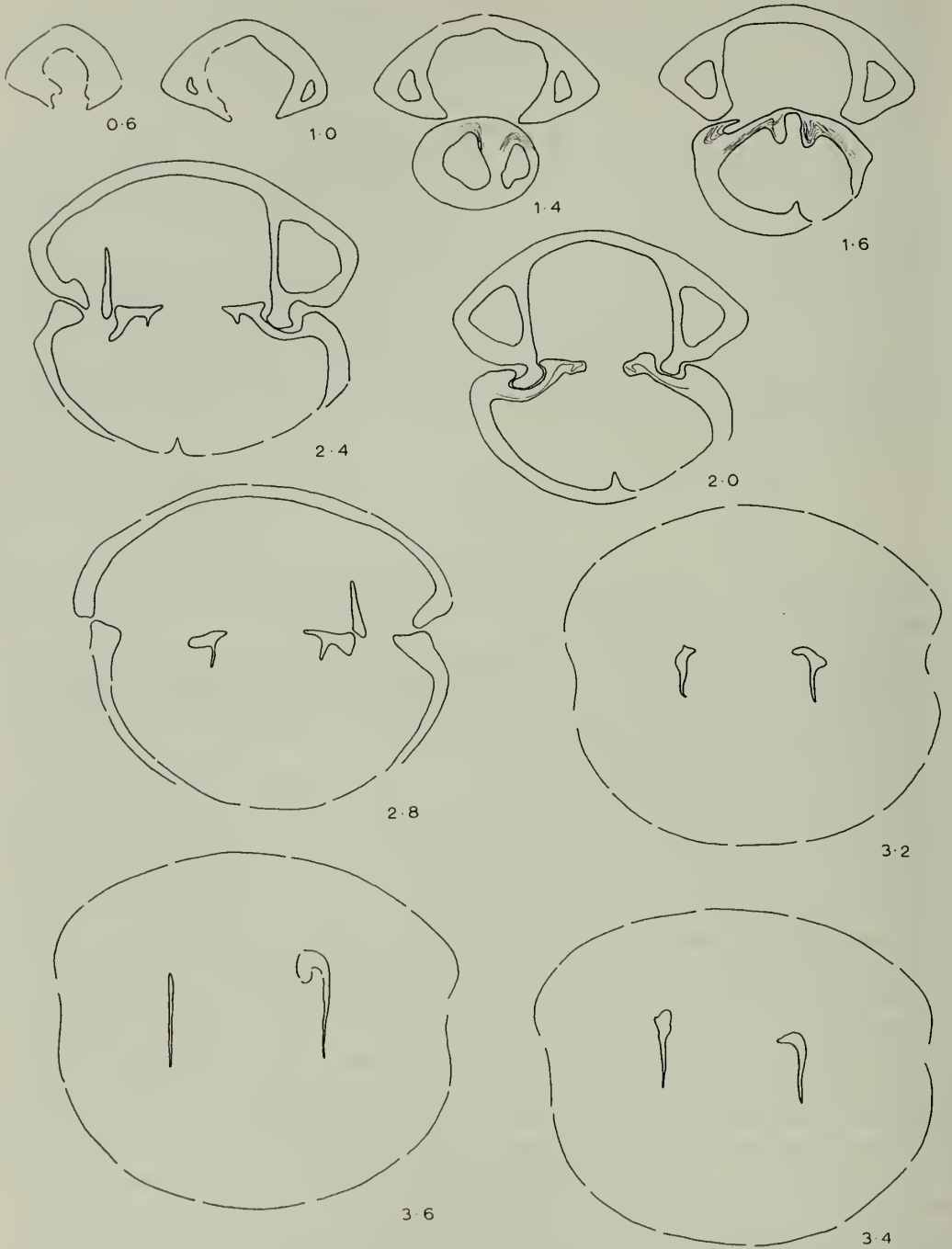


FIG. 19. Transverse serial sections of *Thurmannelia obtvita* (Defrance). Oxfordian. "Terrain à Chailles". Pagny-sur-Meuse (Meurthe et Moselle), France. ($\times 5$).

DISTRIBUTION. The species occurs quite widely in the lower Oxfordian of the northern rim of the Paris Basin, in the northern part of the French Jura and in the Swiss Jura around Basel. *T. obtrita* seems to be co-extensive with the "Terrain à Chailles"; whether it is equally widespread within the *Renggeri* Marls is not known, although the remarks of Loriol (1900) would suggest that it is.

OCCURRENCE. The species has been collected in quantity from two horizons represented by three markedly differing lithologies. The lower horizon is represented by the *Renggeri* Marl, which is a dark coloured calcareous clay. The specimens collected showed a very wide range of size and it is presumed that all except the very youngest stages are present. It seems reasonable to assume that the Marl was deposited in a fairly low energy environment.

The *Renggeri* Marl belongs to the *mariae* zone, while the higher horizons at which *T. obtrita* occurs are in the *cordatum* and *transversarium* (lower part) zones. The two distinctive lithologies occurring in the upper zones are the stratigraphically equivalent "Terrain à Chailles", a sandy limestone with nodular layers of silica, and the self explanatory "oolithe ferrugineuse".

The specimens of *T. obtrita* found in the "Terrain à Chailles" tend to be considerably larger than those from the Marls, both in average size and in the absolute size of the largest specimens; it is also noticeable that there are fewer of the very small individuals. It is suggested that the average size of the specimens within the species probably increased through its stratigraphical range and that the larger size of the specimens from the "Terrain à Chailles" is emphasized by the higher energy environments which is assumed from the lithology; the smaller shells were probably carried away.

The "Terrain à Chailles" is coarsely bedded and the tops of the bedding planes are rather nodular and often show evidence of burrowing activity. *T. obtrita* is found predominantly on these nodular surfaces, where it occurs both singly and in groups. Nearly all the specimens are present with complete, articulated shells, suggesting that they were not transported far before burial; this assumption is supported by the very delicate nature of the test.

From the thin shell and the large, obviously functional pedicle opening, it is suggested that the individuals may possibly have lived attached to weed and that on death they became detached and dropped to the bottom. The groups could be either post-mortem accumulations washed together or possibly small colonies which were deposited together from the same fronds of weed; if they in fact adopted that mode of life. The "Terrain à Chailles" deposits are thought to have accumulated in water no deeper than about 10 fathoms and possibly quite close to the shore line.

The above remarks on the "Terrain à Chailles" are probably also largely applicable to the "oolithe ferrugineuse", which is about 7 m thick in the area of Verdun where the specimens were collected. The bed is only poorly exposed, largely in old shell craters, and collecting from it was relatively difficult. *T. obtrita* does not seem to be so abundant as in the "Terrain à Chailles", but the specimens are about the same size. Associated fauna included terebratulids, irregular echinoids (?*Collyrites*), and lengths of *Millerecrinus*.

REMARKS. The considerable confusion as to the correct nomenclature of the species has largely arisen through the inadequacy of the original descriptions. The name *obtrita* was first used in 1828 by Defrance in the "Dictionnaire des Sciences Naturelles"; the description was very generalized and while no figure was given, he referred to plate 241, fig. 5 in the "Encyclopedie Méthodique". This latter figure is not sufficiently clear for specific identification, although the specimen represented certainly belongs within the *Thurmannella*, *Rhynchonelloidella*, *Ivano-viella* group. While the specimen figured in the "Encyclopedie" is not named or geographically located, in 1820 Schlotheim remarked that it was similar to his *Terebratulites varians*; this fact is also of interest in that the volume of the "Encyclopedie" in which the figure appeared is generally stated to have been published in 1827.

The name *Thurmanni* first appears in Thirria's (1833) work "Statistique Minéralogique et Géologique du Département de la Haute-Saône", in which the palaeontological identifications were given by Voltz. There is no description or figure and the name only occurs in the faunal lists for the "argile avec chailles" and "marne moyenne avec minerai de fer oolithique". The first adequate figure of the species is by Boyé (1842) in his "Importance de l'Etude des Fossiles pour la Reconnaissance géologique des Terrains"; again there is no description and the only information given is that *T. Thurmanni* occurs infrequently in "la marne oxfordienne". Boyé placed this between the "Chailles" and the "Dalle nacrée", making it almost certainly the "*Renggeri* Marls" of present nomenclature.

Between 1828 and 1884 the name *obtrita* does not appear to have occurred in the literature, contrasting with *thurmanni* which was widely used, and the species was well figured by several authors under that name. However, in 1884 Deslongchamps published a paper in which he redefined the species originally described by Defrance (1828), using specimens from the Defrance collection. In this work Deslongchamps admitted that the figure in the "Encyclopedie" cited by Defrance was not clear but went on to say that virtually all the specimens of Defrance labelled as *obtrita* belonged to the form subsequently named *thurmanni*. Deslongchamps considered some of the Defrance specimens to have come from the "Terrain à Chailles" of "Bourgogne or Franche Compté", and not from near Brussels as stated by Defrance, while others came from Lons-le-Saunier, Besançon and Mézières. He then fully described the species, i.e. *obtrita*, and figured three specimens. However, while it is assumed that the figured specimens were from the Defrance collection, this is not certain as a copy of the original work is not available at the British Museum. It is presumed from contemporary synonymies that Deslongchamps produced this paper, with its two plates and their explanations, as a separate publication in 1884.

When the paper on the Defrance species was published in the "Bulletin de la Société linnéenne de Normandie" in 1885, for some reason the explanations to the plates were omitted. From the remarks of Deslongchamps, there seems little doubt as to what Defrance understood by *obtrita* even though this was not clearly stated in his original description. It is presumed that the Defrance collection, which was at Caen, was destroyed together with the Deslongchamps collection during the invasion of Normandy in 1944.

Since the Deslongchamps paper, most authors, with the notable exception of Haas (1889), have continued to use the name *thurmanni*. Rollier (1917) suggested that the name *obtrita* should be abandoned and at the same time proposed the restriction of the name *thurmanni* to the smaller forms as typified by the material from the "Terrain à Chailles" in a new species *silicola*. To the present author, this arbitrary division seems to have little justification, apart from being inadmissible on the grounds of priority.

In setting up his new subgenus *Thurmannella*, Leidhold (1920) included only two species, namely *T. obtrita* and *T. thurmanni*, nominating neither as type of the genus. These two 'species' were differentiated on the grounds that the valves of *T. obtrita* were less inflated and that the uniplication was less developed than in *T. thurmanni*; however, as they occur together at the same horizon and localities and as the features mentioned above show complete gradation between the 'end members', it is here considered that Leidhold was in fact dealing with one species. The synonymy given by Leidhold for his two species is interesting in that he placed *T. thurmanni* of Boyé in synonymy with *T. obtrita* of DeFrance, so separating it from *T. thurmanni* of Voltz; the grounds on which this decision was made are not made clear.

It is concluded that the name *obtrita* of DeFrance has priority over *thurmanni* of Voltz and that *T. obtrita* should be regarded as the type species of *Thurmannella*.

Thurmannella acuticosta sp. n.

(Pl. 5, figs. 10-11, text-fig. 20)

1878 *Rhynchonella varians* var. *Thurmanni* (Voltz); Davidson: 215-16, pl. 28, figs. 14-16.

1933 *Rhynchonelloidea thurmanni* Arkell: 432.

NAME. Latin, *acutus*-a-um—sharp, pointed; *costa*-ae—a rib; the species has very sharp ribs.

DIAGNOSIS. Medium sized *Thurmannella*; about 17-18 relatively coarse, steep, subangular ribs; possesses only very limited posterior smooth area; *crura calcarifer*.

STRATIGRAPHICAL RANGE. Lower Oxfordian—*mariae* zone and lower *cordatum* zones.

TYPE SPECIMEN. Holotype selected is the specimen figured Davidson (1878) pl. 28, fig. 16.

DIMENSIONS OF HOLOTYPE. Length 1.61 cm, thickness 1.46 cm, width 1.74 cm.

DESCRIPTION. *External characters*. The shell outline is subpentagonal to weakly trilobate, the latter condition resulting from the very strongly developed uniplication shown by some specimens. The uniplication in the anterior commissure is emphasized by the strong, steep nature of the subangular ribs. No concentric ornament has been observed.

The beak is sharp and suberect to erect; the erect condition is much less common than in *T. obtrita* and, in comparison with that species, the interarea is smaller and less incurved. An oval, submesothyridid pedicle opening is present; the details of

the deltidial plates have not been satisfactorily observed. The smooth area on the brachial valve is restricted to not more than the posterior quarter of the valve.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.43 cm	1.10 cm	1.60 cm
1.44 cm	1.12 cm	1.67 cm

Internal characters. The preservation of the available specimens is very poor and it was found that the internal features of the first specimen were completely obliterated by partial silicification. A second specimen was sectioned and the structures,

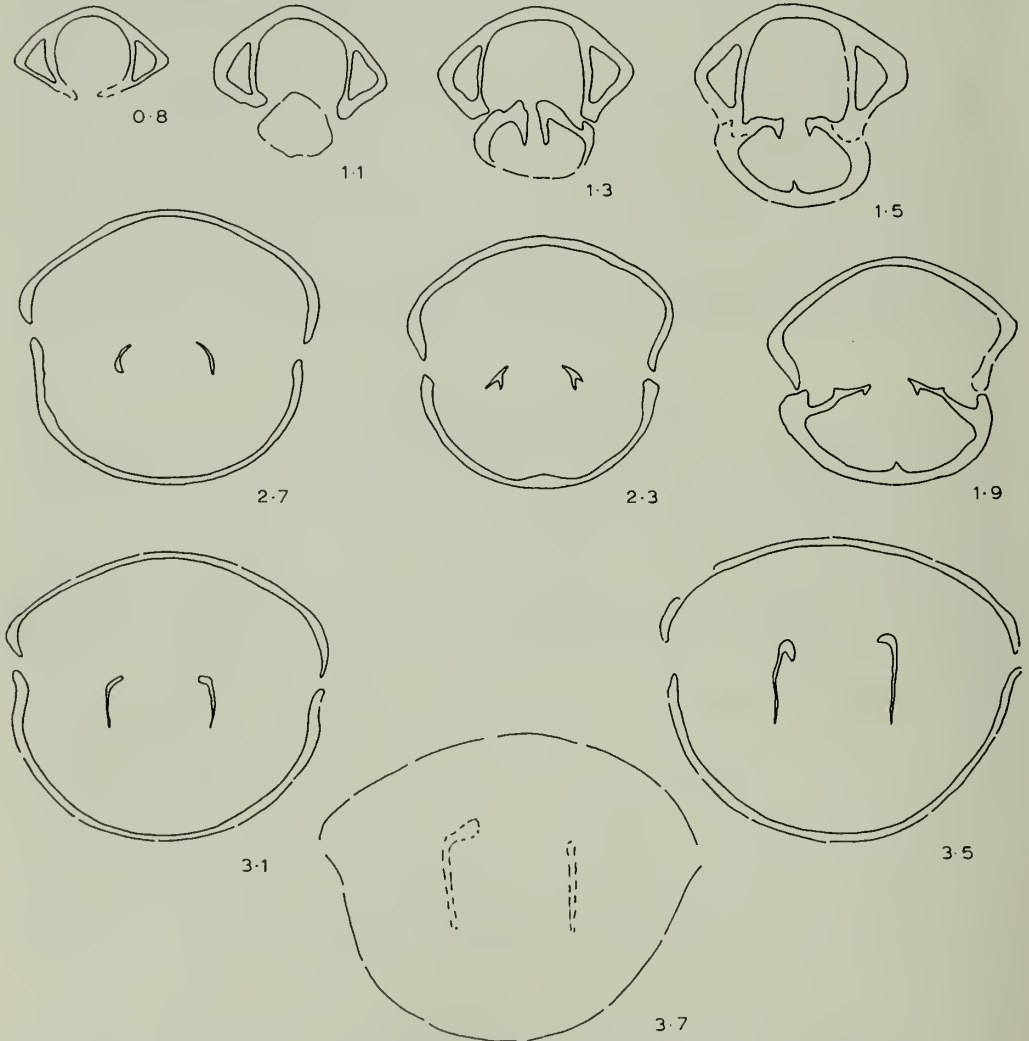


FIG. 20. Transverse serial sections of *Thurmannella acuticosta* sp. nov. Oxfordian. Lower Calcareous Grit. Filey Brigg, Yorks. ($\times 5$).

although still only poorly preserved, appeared to show no notable differences from those described above for *T. obtrita*.

DISTRIBUTION. *T. acuticosta* is one of the most common species in the Lower Calcareous Grit of Yorkshire but, according to Arkell (1933), it has only been recorded from two localities in the south of England, namely, at Catcombe, near Lyneham, and in one of the Kent borings.

OCCURRENCE. The Lower Calcareous Grit appears to be very similar to the "Terrain à Chailles", as developed in the *cordatum* and lower *transversarium* zones of northern France, with the exception of the abundance of "*Spongia paradoxica*" (=the trace fossil *Thalassinoides teste* Ager), as seen at Filey Brigg. It would appear that the environment represented is again of the nearshore, high energy type.

Subfamily **ACANTHOTHYRIDINAE** Schuchert, 1913
Genus **ACANTHOTHIRIS** Orbigny

- 1850 *Acanthothiris* Orbigny, 323.
- 1875 *Acanthothyris* Orbigny: Paetel, 1.
- 1877 *Acanthothiris* Dall, 11.
- 1886 Gruppe der Spinosen Rothpletz, 93.
- 1889 *Acanthothyris* Orbigny: Buckman and Walker, 41.
- 1894 *Acanthothyris* Orbigny: Hall and Clarke, 836.
- 1914 *Acanthothiris* Orbigny: Buckman, 2.
- 1917 *Acanthothyris* Orbigny: Rollier, 74.
- 1918 *Acanthothiris* Orbigny: Buckman, 70.
- 1929 *Acanthothiris* Orbigny: Schuchert and Le Vene, 26.
- 1936 *Acanthothyris* Orbigny: Muir-Wood, 27.
- 1960 *Acanthothiris* Orbigny: Ager, 157.
- 1960 *Acanthothyris* Orbigny: Makridin, 256.
- 1963 *Acanthothiris* Orbigny: Seifert, 168.
- 1965b *Acanthothiris* Orbigny: Ager, H611.

TYPE SPECIES. *Terebratulites spinosus* Schlotheim, designated by Rollier (1917). This is regarded by the author as a synonym of *Anomia spinosa* Linnaeus (1767) and is discussed below.

EMENDED DIAGNOSIS. Small to medium sized sub-pentagonal or laterally oval rhynchonellids; biconvex; uniplicate with low dorsal fold; many well developed ribs, several of which bifurcate; test covered by hollow spines which arise from the crests of the ribs; beak small and erect or slightly incurved; well developed groove ("pedicle trough") running from posterior of pedicle opening to tip of beak; fairly strong median septum present; crura radulifer.

STRATIGRAPHICAL RANGE. ? Aalenian, Bajocian—Bathonian/basal Callovian.

DESCRIPTION. *External characters.* The larger acanthothirids tend to be more globose than the smaller; the brachial valve is more inflated than the pedicle. The many well marked, rather shallow, sub-rounded ribs tend to bifurcate laterally and from their crests arise the long, slender, hollow spines which cover the test. There is a slight fold on the dorsal valve and a rounded uniplication in the anterior commissure. The beak is relatively small and sufficiently incurved to obscure the

details of the pedicle opening and deltidial plates. Beak ridges and interarea are present but rather variable in development. The young forms tend to be sub-trigonal to subcircular.

Internal characters. Pedicle valve. The delthyrial cavity is quadrate in transverse section, but in the initial posterior sections there is a low dorsally directed ridge. This results from the presence of a groove which is situated on the anterodorsal side of the beak and runs from the pedicle opening to the tip of the beak. This structure appears to be a pedicle collar as originally defined by Thomson (1927); it is not, however, the structure defined as a pedicle collar in the "Treatise" (1965), and is here referred to as the "pedicle trough".

The lateral cavities are relatively narrow and the slender dental lamellae bounding them are either subparallel or slightly divergent ventrally. Teeth and sockets are both crenulated.

Brachial valve. A median septum is quite well developed. A septalium is not present but the median structure, dorsal of the ventrally arched hinge plates, seen in *A. spinosa* and *A. cf. A. costata* could possibly have resulted from the fusion of septalial plates. Crural bases are hardly differentiated. The crura are of the radulifer type and tend to be oval or flattened in the plane of articulation, as seen in transverse section. Muscle scars have not been observed and even Buckman (1918) commented that they were obscure in both valves.

SPECIES. As well as *A. spinosa* and *A. cf. A. costata*, here described, the literature abounds with descriptions and names of spinose rhyntonellids of this age. The following nominal species are provisionally attributed to this genus :

- A. balinensis* Rollier (1917, p. 77)
- A. broughensis* Muir-Wood (1952, pl. 123, p. v, figs. 11, 13-15)
- A. crossi* (Walker) (1869, p. 215)
- A. costata* Orbigny (1850, p. 286)
- A. doulingensis* (Richardson and Walker) (1907, p. 426, pl. xxvii, fig. 2)
- A. elargata* Seifert (1963, p. 170, pl. x, fig. 8)
- A. globosa* Buckman (1918, p. 918, pl. xix, fig. 25)
- A. inflata* (Quenstedt) (1868, p. 112, pl. xxxix, figs. 46-47)
- A. midfordensis* (Richardson & Walker) (1907, p. 427, pl. xxvii, fig. 1)
- A. multispinosa* Seifert (1963, p. 172, pl. x, fig. 12)
- A. oligacantha* (Branco) (1879, p. 127, pl. vi, figs. 6-7)
- A. paucispina* Buckman and Walker (1889, pp. 52-53)
- A. powerstockensis* Buckman and Walker (1889, p. 52)
- A. radwanowiczensis* Rollier (1917, p. 77)
- A. sentosa* (Quenstedt) (1868, p. 113, pl. xxxix, figs. 55-56)
- A. sinuata* (Quenstedt) (1868, p. 114, pl. xxxix, fig. 59)
- A. subglobosa* Seifert (1963, p. 171, pl. x, fig. 11)
- A. tenuispina* (Waagen) 1867, p. 640, pl. xxxii, fig. 6).

DISTRIBUTION. *Acanthothiris* is a common genus occurring widely throughout the Middle Jurassic rocks of Europe, including those of England, Normandy, the French, Swiss and German Jura and Poland.

OCURRENCE. The genus has been collected by the author only from coarse, bioclastic limestone.

REMARKS. On account of their distinctive appearance members of *Acanthothiris* have been described and figured on numerous occasions, usually under the name of *Rhynchonella*, *Terebratula* or *Acanthothiris spinosa*. The author has not attempted to disentangle the nomenclature and synonymy of these numerous descriptions and figures, but has here only attempted to define and clarify the type species together with *A. cf. costata*, which happened to be a very common fossil in the part of the southern French Jura mapped by members of Imperial College. The latter species was investigated in order to obtain a wider knowledge of the variation of internal structures of the genus as these are not adequately described in the literature.

***Acanthothiris spinosa* (Linnaeus)**
(Pl. 5, figs. 12-17, text-figs. 21-22)

- 1767 *Anomia spinosa* Linnaeus: 1154.
 1768 (concha) *anomonia ventricosa*, *striata echinata*, d'Annone in Knorr and Walch: 90, pl. B4, fig. 4.
 1779 *Anomia* Walcott: 21, fig. 31.
 1813 *Terebratulites spinosus* Schlotheim: 73.
 1813 *Anomia spinosa* Linnaeus; Townshend: 372.
 1817 *Terebratula spinosa* Smith: 108.
 1820 *Terebratulites spinosus* Schlotheim: 269.
 1825 ?*Terebratula aspera* Koenig: fig. 219.
 1829 *Terebratula spinosa* Townshend and Smith; Phillips: 123, pl. 9, fig. 18.
 1833 *Terebratula spinosa* Buch: 58-59.
 1838 *Terebratula spinosa* Buch: 161-62, pl. 6, fig. 4.
 1850 *Hemithiris spinosa* Orbigny: 268.
 1850 *Acanthothiris spinosa* Orbigny: 323.
 1851 *Rhynchonella spinosa* (Schlotheim); Davidson: 71-73, pl. 15, figs. 15-20.
 1857 *Rhynchonella spinosa* (Schlotheim); Deslongchamps: 355-56, pl. 5, fig. 1.
 1858 *Rhynchonella spinosa* (Schlotheim); Davidson: 222.
 1882 *Rhynchonella spinosa* (Schlotheim); Buckman: 40-41.
 1889 *Acanthothyris spinosa* (Linnaeus); Buckman and Walker: 12-14.
 1900 *Acanthothyris spinosa* (Schlotheim); Greppin: 178-80, pl. 19, fig. 3.
 1917 *Acanthothyris spinosa* (Schlotheim); Rollier: 76-77.
 1918 *Acanthothiris spinosa* (Linnaeus); Buckman: 70-72, pl. 19, fig. 26.
 1936 *Acanthothiris spinosa* (Linnaeus); Muir-Wood: 28.
 1936 *Acanthothyris spinosa* (Schlotheim); Arcelin and Roché: 54-58, pl. 1, figs. 1-18, pl. 12, fig. 2.
 1959 *Acanthothyris spinosa* (Schlotheim); Henry: 119-21.
 1966 *Acanthothiris spinosa* (Schlotheim); Alméras: 277-79, pl. 17, figs. 1-3.

EMENDED DIAGNOSIS. Medium to large sized *Acanthothiris*; relatively globose; relatively subpentagonal; brachial valve considerably more inflated than the pedicle; "pedicle trough" present; well marked uniplication; 30-35 ribs on each valve; crura radulifer.

TYPE SPECIMEN. Neotype, here proposed, is the specimen in the collection of the B.M.(N.H.) from the Inferior Oolite of Rodborough Hill numbered B4030. The

exact horizon is not given but it is probably from the Upper Trigonía Grit, i.e. the *parkinsoni* zone of the Bajocian.

STRATIGRAPHICAL RANGE. Upper Bajocian to Upper Bathonian/Lower Callovian.

DIMENSIONS OF NEOTYPE. Length 2.14 cm, thickness 1.71 cm, width 2.37 cm.

MATERIAL. 30 specimens from the collection of the B.M.(N.H.) ; 23 specimens from Normandy and 9 from Switzerland in the collection of the author in the British Museum (Nat. Hist.) nos. BB. 45682-89.

DESCRIPTION. *External characters.* Medium to large sized *Acanthothiris* which is characteristically fairly globose. In early growth stages the two valves are of almost equal convexity but, in adult forms, the brachial valve is much the more inflated. Young forms have a subcircular to subtrigonal outline, which becomes modified to the subpentagonal shape of the adult. The width is usually, but not invariably, greater than the length. There is a marked, rounded uniplication in the anterior commissure, accompanied by a low fold on the brachial valve.

In early growth stages, the beak tends to be small, acute and erect ; it becomes more incurved in the adult and often obscures the pedicle opening and deltidial plates. The deltidial plates, as seen in the serial sections, are conjunct ; the pedicle opening is submesothyridid. Beak ridges are quite well developed and limit the incurved interarea.

The test ornament consists of about 30 to 35 subangular to subrounded ribs, as counted at the anterior commissure ; these ribs may bifurcate once or twice, rarely more, and occasional ribs are inserted by intercalation. The long, slender spines which form the most distinctive feature of the genus arise from expanded bases situated along the crests of the ribs. Spines of up to 1 cm have been observed still attached to the test ; however, in most specimens they are indicated only by the presence of low spine bases. Although they are hollow, they do not seem to have had any direct connection with the mantle. The other ornament consists of rather weak growth lines, which are usually only seen in the inter-rib troughs of well preserved material, and occasional growth lamellae.

Davidson (1858) suggested that, " when alive, *R. spinosa*, was more or less coloured with red ; at least, we have seen specimens in which the spines had preserved that colour ; this is also the opinion of M. Deslongchamps". This observation was probably founded largely on material from quarries near Caen in Normandy and, while true, omits to point out that large numbers of other organisms are also so coloured and this would appear to be due to some local factor rather than to original colouration. Dr. Rioult, (personal communication, 1964) suggested that this colouration is due to algae.

DIMENSIONS OF FIGURED ADULT SPECIMENS.

length	thickness	width
2.28 cm	1.78 cm	2.37 cm
2.14 cm	1.71 cm	2.37 cm
2.42 cm	2.05 cm	2.88 cm

Internal characters. Pedicle valve. The development of the deltidial plates, showing the crumpling together characteristic of the species, is clearly illustrated in

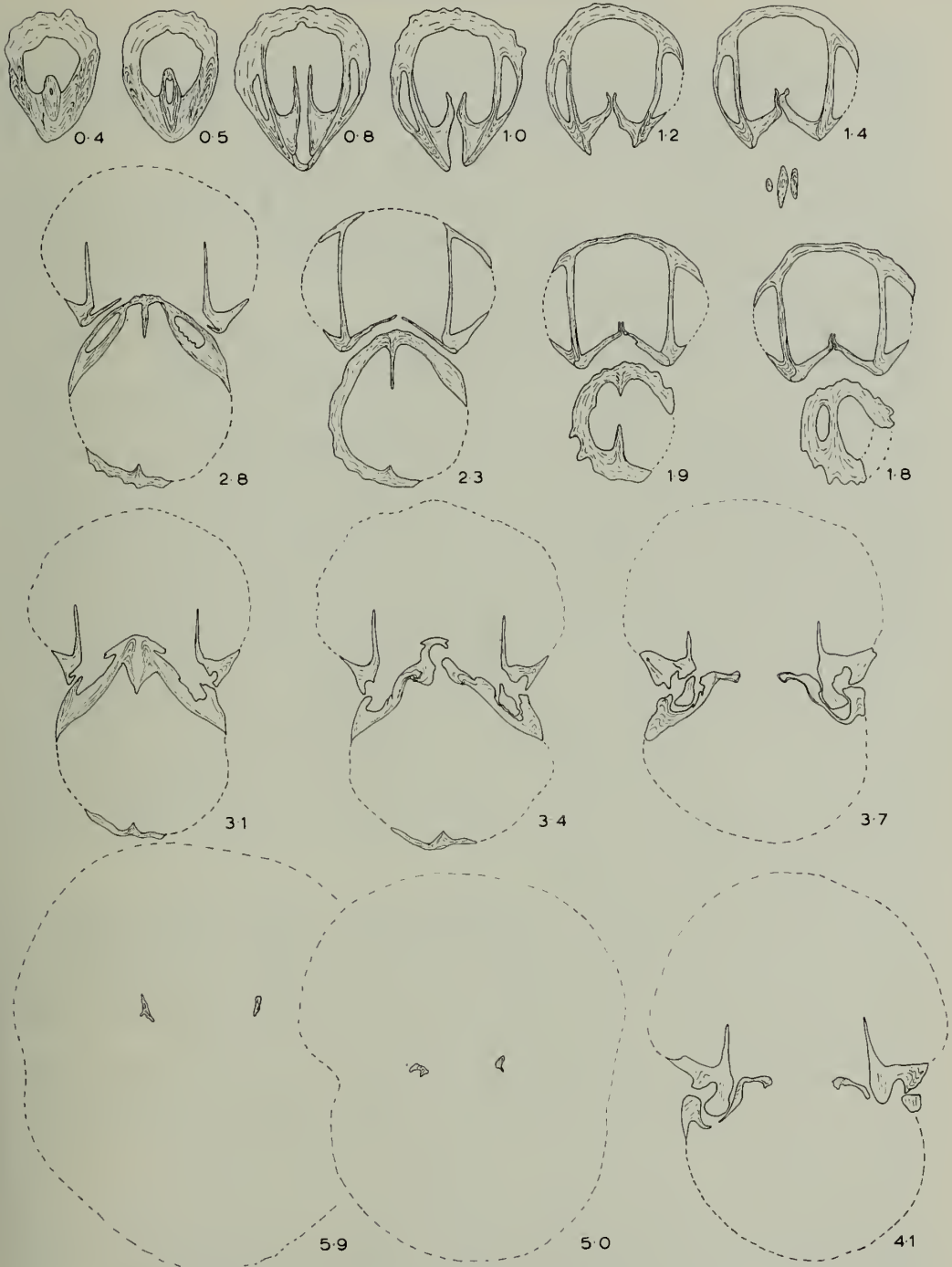


FIG. 21. Transverse serial sections of *Acanthothiris spinosa* (Linnaeus). Bajocian. Upper *Trigonia* Grit. Wooton-under-Edge, Glos. ($\times 4$).

the serial sections. The pedicle opening can be seen at the base of the pedicle groove ; the difference in appearance of this structure, as compared with *A. cf. costata* results from the greater incurvature of the beak in *A. spinosa*.

Brachial valve. See generic description. The shape of the crura seems to be a useful criterion for differentiating the species from *A. cf. costata*.

DISTRIBUTION. The species has been definitely recorded from the Cotswolds, Normandy, northern France, around Basel in Switzerland and from Monsard (Saône et Loire). The name *spinosa* has been used frequently in the past for any spinose rhynchonellid and consequently from the literature, it is very difficult to ascertain the true distribution of *A. spinosa* s.s.

OCCURRENCE. The species is considered to have lived under conditions similar to those described for *A. cf. costata*.

REMARKS. The rhynchonellid now known as *Acanthothiris spinosa* s.s. was first figured by Knorr and Walch (1768) with the description, "concha anomia, ventricosa, striata echinata", which was given by Professor d'Annone. A specimen regarded by Rollier (1917) as the type of Knorr and Walch is preserved in the Naturhistorisches Museum of Basel ; however, as Rollier pointed out, this specimen differs markedly from the original figure in such features as the number of ribs, of which the specimen has 36-38 on the pedicle valve rather than the 26 figured. This discrepancy is such that Dr. Gasche, of the Museum, is of the opinion (personal communication 1965), that this is not the original of the Knorr and Walch figure and the present author would concur with this observation.

Linnaeus (1767)* described *Anomia spinosa*, stating that it had long spines and that it came from England. Although, unfortunately, the original is not preserved in the Linnaeus Collection, at present in the B.M.(N.H.), it seems reasonable to assume that the *A. spinosa* referred to by Linnaeus is the very common Inferior Oolite species of *Acanthothiris*. This was the view taken by Muir-Wood in her 1936 monograph. Therefore, it has been decided to define the species with a neotype from the Bajocian of the Cotswolds.

The confusion over the authorship of the species has arisen mainly as a result of Schlotheim (1813) mentioning a *Terebratulites spinosus*, which he did not figure or describe, but merely referred to the figure of Knorr and Walch. As this figure was not named in the correct binomial form and as it is regarded by the present author as conspecific with *Anomia spinosa* of Linnaeus, the Schlotheim name must be regarded as a synonym and the species attributed to Linnaeus.

In 1889 Buckman and Walker fully discussed the earlier literature and redescribed all the known British spinose rhynchonellids. Rollier added to the confusion by setting up many new species based purely on published figures, many of which were wholly inadequate in the first place. Buckman (1918) redefined the genus and

* This is the first edition in which *spinosa* is described and at the end of the remarks on habitat, which mention that the species occurs in England, is written "Solander". Daniel Carl Solander was an associate of Linnaeus but it is not clear whether, by placing Solander's name after the remarks Linnaeus was suggesting that he was the author of the species or whether he was merely quoting Solander in stating that the species occurred in England. All subsequent authors who have referred to the "Systema Natura" have attributed the name *spinosa* to Linnaeus.

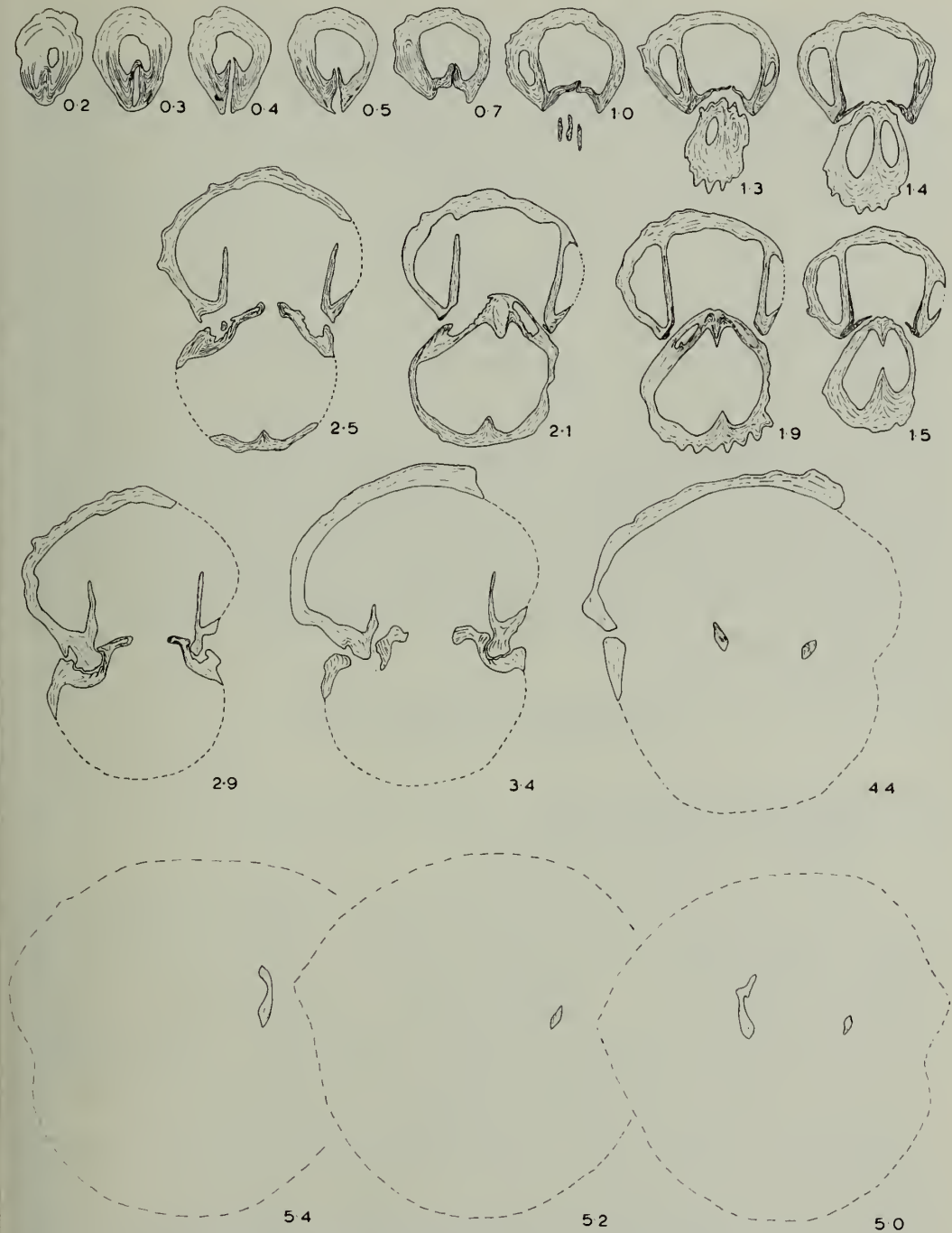


FIG. 22. Transverse serial sections of *Acanthothiris spinosa* (Linnaeus). Bathonian. "Var-ians Schichten", Liestal, Basel, Switzerland. ($\times 4$).

although no specific description of *A. spinosa* was given, he figured a specimen of *A. spinosa* s.s. from the Inferior Oolite of Midford near Bath.

There was no further discussion of the species until 1936 when Arcelin and Roché attempted to disentangle the synonymy, but failed to take account of the literature prior to Schlothheim. They described and figured a beautiful series of silicified specimens from the Bajocian of Monsard (Saône et Loire); these specimens have been examined in the collection of the University of Lyon and appear to belong to *A. spinosa* s.s., although it is difficult to compare the internal structures with those of the sectioned material. Also in 1936 Muir-Wood discussed the type of the genus, concluding it to be the species referred to by Linnaeus and that this was the "common Inferior Oolite species"; in doing this, however, she appears to have overlooked the earlier designation of Rollier. She also stated that she considered the *spinosa* of Linnaeus to be congeneric but not conspecific with the form described by Knorr and Walch from Muttentz, as specimens from that area were "larger and more globose".

The area of Muttentz now being an industrial suburb of Basel, it is not possible to obtain exactly topotypic material; however, within a few kilometres there are good exposures of the Upper Bathonian Varians-Schichten from which the original is presumed to have come and the author visited one such exposure at Liestal, collecting a good sample of specimens. From the examination of this material, the author believes that it should be considered as conspecific with the English species from the Inferior Oolite; specimens from both areas have been sectioned, see text-figs. 21, 22 and are identical internally.

Acanthothiris cf. *costata* Orbigny

(Pl. 6, figs. 2-4, text-fig. 23)

1850 *Hemithiris costata* Orbigny: 286-87.

1850 *Acanthothiris costata* Orbigny: 323.

1910 *Hemithiris costata* Orbigny; Thevenin: 100, pl. 20, figs. 18-20.

1917 *Acanthothyrus costata* (Orbigny); Rollier: 74.

1918 *Acanthothiris costata* Orbigny; Buckman: 71.

EMENDED DIAGNOSIS. Medium sized *Acanthothiris*; width always greater than length; outline sub-oval; 25-30 low, rounded ribs; beak small and tightly pressed to the brachial valve; crura radulifer.

STRATIGRAPHICAL RANGE. d'Orbigny's material came from the "Bajocien", while the specimens here described are of Upper Bathonian/Lower Callovian age.

MATERIAL. Numerous specimens collected by the author and various members of Imperial College from the southern French Jura. 20 specimens in the author's collection in British Museum (Nat. Hist.) nos. BB. 45690-45709.

DESCRIPTION. *External characters.* The width is always greater than the length, resulting in a laterally suboval outline. The beak is very small and closely adpressed to the brachial valve; no pedicle opening or deltidial plates are visible externally in the adult specimens. Beak ridges and interarea are both poorly developed. Adult specimens have between 25 and 30 ribs, as counted at the anterior

commissure. These ribs are rather rounded in cross section and frequently bifurcate once or twice over their length ; ribs are also occasionally inserted by intercalation. The ornament also includes growth lines, but these are not strongly developed and are only seen on well preserved material. Long, slender spines arise from the crests of the ribs and are fairly evenly distributed over the test ; the hollow nature of these is clearly seen in the serial sections. There is a low rounded uniplication in the anterior commissure ; however, any accompanying fold in the brachial valve is only poorly developed.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.96 cm	1.45 cm	2.57 cm
1.87 cm	1.38 cm	2.50 cm
1.84 cm	1.15 cm	2.30 cm

Internal characters. Pedicle valve. The deltidial plates, as seen in serial section, are very weakly developed, as compared with *A. spinosa*, and do not meet and become crumpled together. The nature of the "pedicle trough" is clearly seen but from the incurvature of the valve it could obviously have been functional only during the early stages of ontogeny as proved by the inflation of the brachial valve and the incurvature of the beak which must have lead to atrophy of the pedicle in adults. The dental lamellae diverge slightly ventrally and limit a subquadrate delthyrial cavity. The teeth are strong and crenulated.

Brachial valve. The median septum is quite strongly developed. There is no septalium as the septalial plates, although present, are very weak. Crural bases are not differentiated. The crura are radulifer and curve distally toward the pedicle valve ; at their proximal ends they are rather flattened in cross section and lie in the plane of articulation.

DISTRIBUTION. The material on which Orbigny based his original description came from Gueret (Sarthe) ; all the specimens described by the author came from the southern French Jura (Ain).

OCCURRENCE. Details of the type locality for *A. costata* are not known. The Jura material was collected from the Middle Chanaz Beds (Ager & Evamy, 1963) from the area around Belley (Ain). Dr. Evamy gives the following description of the lithology in his thesis: "irregularly bedded, poorly sorted calc-arenites, characterized . . . by their content of ferruginous oolites. . . . The lower and principal unit . . . consists of irregularly bedded brown and grey limestones and similarly coloured shales". He also notes, "The member (Middle Chanaz Beds) may also be recognized in the field by the abundance of *Acanthothiris*".

The acanthothirids occurred as clusters or "nests" in the limestones and concentrations of them were also noticed in the shales. In both situations the forms were mainly adult with valves intact and, in the majority of cases, with the beaks pointing downwards. It would seem that most of the specimens were not far removed from their life position ; however, some movement or sorting is indicated by the noticeable lack of juvenile forms and the similar lack of in situ spines. It should be noted

that while many of the specimens were in "nests" or associations, either vertical or horizontal, many others occurred singly and scattered through the rock unit. The above mentioned "nests" have been referred to by Ager & Evamy (1963) as seeming, "to be true colonial associations".

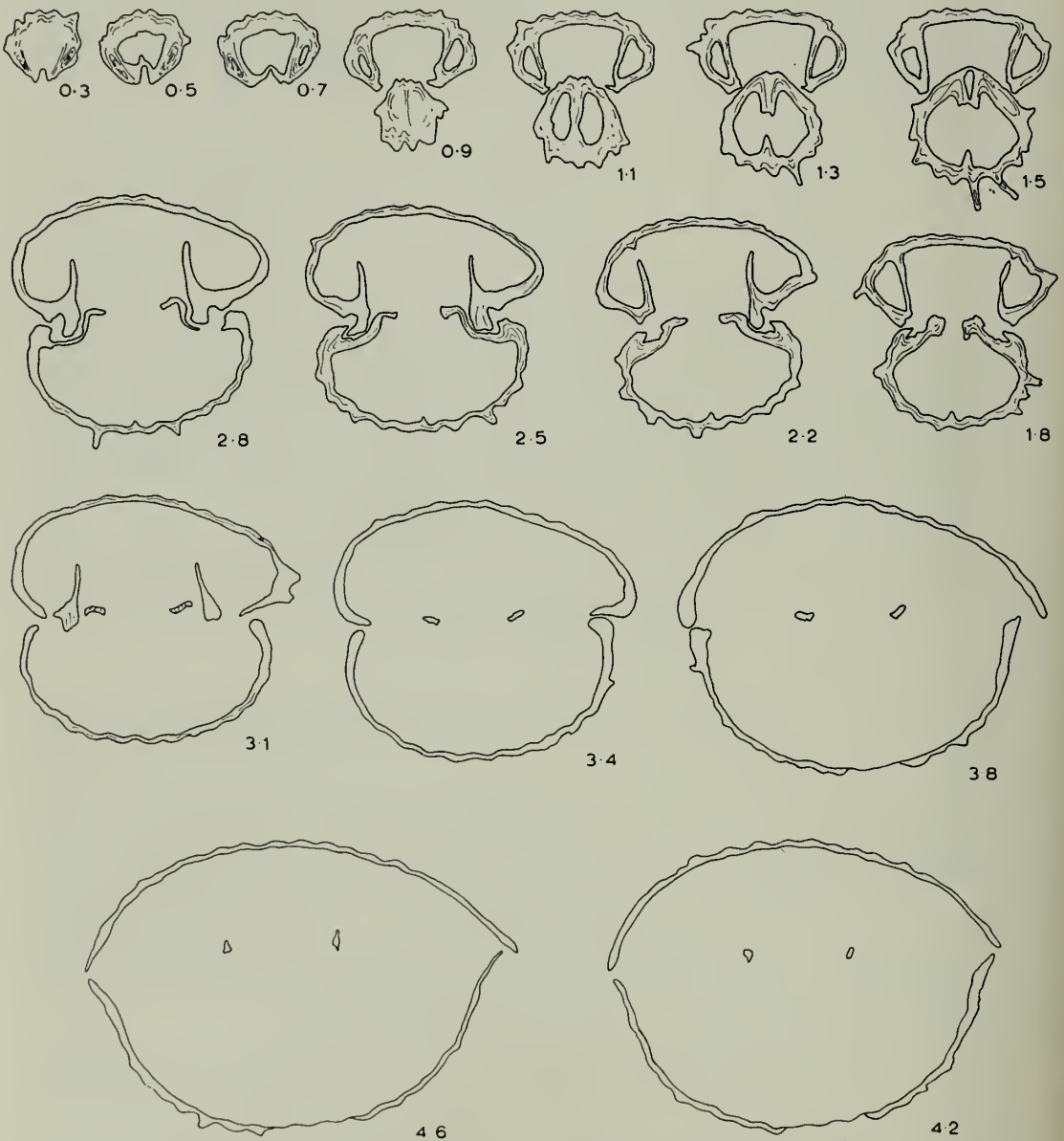


FIG. 23. Transverse serial sections of *Acanthothiris* cf. *costata* Orbigny. Bathonian/Callovian. Middle Chanaz Beds. Pugieu (Ain), France. ($\times 4$).

The evidence of the lithology is such as to suggest a rather high energy environment. Given that the latter deduction is correct, it seems to the author that the spines would have been a useful anchoring device and it is considered that Rudwick (1964) under-estimated this function in proposing a sensory role for them.

REMARKS. A plaster cast of the specimen from the Orbigny collection figured by Thevenin (1910) has been examined, through the kindness of Dr. Fischer of the Jardin des Plantes (Musée d'histoire Naturelle), and externally this closely resembles the material collected from the southern French Jura. However, a conspecific identification has not been given as no topotype material has been sectioned and hence no comparison of the internal structures has been possible. The main difference between the Orbigny specimen and those described from the Jura lies in the rib count; that of the former being 20 while that of the latter is between 25 and 30. As the other two specimens of *A. costata* in the Orbigny collection are only poorly preserved (Dr. D. V. Ager, personal communication 1965), it is not considered reasonable to separate the Jura form as a new species merely on the basis of the slight difference in the number of ribs without an investigation of topotype material of the Orbigny species to ascertain its variation and internal structure.

Genus *ACANTHORHYNCHIA* Buckman

1914 *Acanthorhynchia* Buckman: 2, (nomen nudem).

1918 *Acanthorhynchia* Buckman: 69.

1960 *Acanthorhynchia* Buckman; Makridin: 256.

1965b *Acanthorhynchia* Buckman: Ager: H611.

TYPE SPECIES. *Acanthothyris panacanthina* Buckman and Walker, by original designation.

EMENDED DIAGNOSIS. Small to medium sized rhynchonellids; transversely oval or sub-triangular in outline; thin test covered by numerous fine spine-covered ribs; anterior commissure rectimarginate or with slight uniplication; deltidial plates absent, or reduced and disjunct; crura calcarifer or radulifer.

STRATIGRAPHICAL RANGE. Upper Bajocian—Upper Volgian/Neocomian.

DESCRIPTION. *External characters.* The genus contains a series of small to medium sized rhynchonellids. The smaller species tend to be subtriangular in outline, equally biconvex and generally flatter, while the larger species are transversely oval in outline, more globose and with the brachial valve more inflated than the pedicle.

The anterior commissure may have a slight uniplication in the larger forms, but in the smaller it is usually straight. The beak is relatively small and suberect or erect; deltidial plates are absent in the smaller forms and of a reduced, disjunct variety in the larger. Beak ridges and interarea are never well developed. There are typically one or two well developed growth lamellae, but the finer growth lines have not been observed. The test is covered with many fine, bifurcating ribs, from the crests of which are developed the characteristic, numerous fine spines which project at a low angle.

Internal characters. Pedicle valve. The dental lamellae are apparently only developed in the larger species and, when they are not developed, the teeth tend to be inserted at a very shallow angle.

Brachial valve. A low median septum may be present but septalial plates and a septalium are never developed. The ends of the inner hinge plates show a distinctive thickening and in one species, *A. (Acanthorhynchia) spinulosa*, this results in a structure comparable with a cardinal process. The crura, especially in *A. (Acanthorhynchia) panacanthina*, the only really well preserved species examined, appear to closely resemble the form described by Muir-Wood (1935) as *calcarifer*. However, in other species they seem to more closely resemble the *radulifer* type.

SPECIES. The following nominal species are provisionally recognized as belonging to the genus; a sub-generic designation is given where possible:

- A. davidsoni* (Rollier) (1917, p. 77)
- A. (Echinirhynchia) dealbata* (Rollier) (1917, p. 80)
- A. (Echinirhynchia) fileyensis* (Buckman & Walker) (1889, p. 56)
- A. (Echinirhynchia) impressata* (Rollier) (1917, p. 79)
- A. (Echinirhynchia) lorioli* (Rollier) (1917, p. 79)
- A. (Acanthorhynchia) multistriata* (Kitchin) (1900, pp. 75-77) pl. xiv, figs. 10, 11
- A. (Acanthorhynchia) myriacantha* (Deslongchamps) (1859, p. 251, pl. iv, fig. 12)
- A. nikitensis* Gerasimov (1955, p. 216, pl. xliii, fig. 5)
- A. (Acanthorhynchia) panacanthina* (Buckman & Walker) (1889, p. 53)
- A. (Acanthorhynchia) regans* (Szajnocha) (1879, p. 222, pl. vi, figs. 1, 2)
- A. (Echinirhynchia) senticosa* (Schlotheim) (1820, p. 268)
- A. (Echinirhynchia) silicea* (Quenstedt) (1871, p. 115, pl. xxxix, fig. 66)
- A. (Acanthorhynchia) spinulosa* (Opper) (1858, p. 608)
- A. (Acanthorhynchia) vilsensis* sp. nov.
- A. zieteni* (Rollier) (1917, p. 75).

DISTRIBUTION. Although rare, the genus is very widespread and occurs throughout the French and German Jura, and in Normandy, Poland and England. It has also been recorded from the Kutch.

REMARKS AND OCCURRENCE. The genus was founded by Buckman in 1918, after being mentioned by him in 1914. In his original description, Buckman included most of the species here retained in the genus, together with a few now considered as belonging to *Acanthothiris* or to be of uncertain affinity. Although distinctive, all the included species are rather rare and this has necessitated the use of much borrowed material in order to attempt a complete revision of the genus.

The genus *Acanthorhynchia*, as here defined, includes two distinct groups, based on external morphology, which overlap each other in time and, to a lesser extent, geographical area. It is here proposed to designate these groups as sub-genera, namely *Acanthorhynchia* s.s. and *Echinirhynchia* sub-gen. nov.

As stated above, all the species are rare and details of the source rock and supposed environment are only rarely given in the literature. However, the fact that *A. (Acanthorhynchia) panacanthina* comes from the Inferior Oolite and *A. (Acanthorhynchia) rogans* comes from the Balin Oolite suggests that the sub-genus *Acanthor-*

hynchia s.s. lived in fairly high energy environments. The specimens of *Echinirhynchia* collected from the French Jura came from very fine-grained sediments, either clays or calcutites, while the material recorded from Germany is also either from clays e.g. *Terebratula senticosa impressae* Quenstedt, or from the sponge reef facies e.g. *A. (Echinirhynchia) senticosa* (Schlotheim). The occurrence of the sub-genus in these two markedly different facies may possibly indicate that its mode of life was planktonic or that it lived attached to floating weed ; this hypothesis was suggested by Ager (1965a).

Sub-genus **ACANTHORHYNCHIA** s.s.

TYPE SPECIES. *Acanthothyris panacanathina* Buckman and Walker.

DIAGNOSIS. Medium to large species of *Acanthorhynchia* with a transversely oval to subrounded outline ; either equally biconvex or with a more inflated brachial valve ; deltidial plates and dental lamellae may be present.

STRATIGRAPHICAL RANGE. Upper Bajocian—Upper Volgian/Neocomian.

DISTRIBUTION. The sub-genus has a wide range both geographically and chronologically ; however, the consistent external and internal features of the included species suggest a continuous evolutionary lineage. The extent of the geographical range is given under the species description. Apart from the species described *A. (Acanthorhynchia) multistriata* (Kitchin) is recorded from the "Oomia Group" of the Kutch and *A. (Acanthorhynchia) rogans* (Szajnocha) occurs in the "Balin Oolite" of Poland.

A. (*Acanthorhynchia*) *panacanathina* (Buckman and Walker)

(Pl. 6, figs. 5-7, text-fig. 24)

1851 *Rhynchonella senticosa* (Buch); Davidson: 73-74, pl. 15, fig. 21.

1878 *Rhynchonella senticosa* (Buch); Davidson: 223.

1878 *Rhynchonella senticosa* (Buch); Davidson: 85, pl. 4, fig. 20.

1882 *Rhynchonella senticosa* (Buch); Buckman: 41-42.

1889 *Acanthothyris panacanathina* Buckman and Walker: 53-54. [= *A. Davidsoni* Rollier 1917].

1918 *Acanthorhynchia panacanathina* Buckman and Walker; Buckman: 69-70, pl. 19, fig. 23.
[= *A. Davidsoni* Rollier 1917].

EMENDED DIAGNOSIS. Large *Acanthorhynchia* which ranges in size up to 3.05 cm long, 2.20 cm thick and 3.53 cm wide. Biconvex and transversely suboval in outline ; beak suberect ; deltidial plates narrow, trigonal and disjunct ; anterior commissure sinuate ; crura calcarifer.

STRATIGRAPHICAL RANGE. Bajocian—probably restricted to the *parkinsoni* zone.

TYPE SPECIMEN. In their synonymy Buckman and Walker (1889) mention the specimen figured by Davidson (1851) on pl. 15, fig. 21 and it seems reasonable to take this as the type of the species. B 12082 (B.M. (N.H.))

DESCRIPTION. *External characters.* This is the largest known species of *Acanthorhynchia*. The test is covered with fine ribs ; Buckman and Walker cite a specimen as having about a hundred ribs on each valve, with forty spines on each rib. This statement seems to be essentially correct, although the fineness of the features concerned is such as to preclude accurate counting except on well preserved and

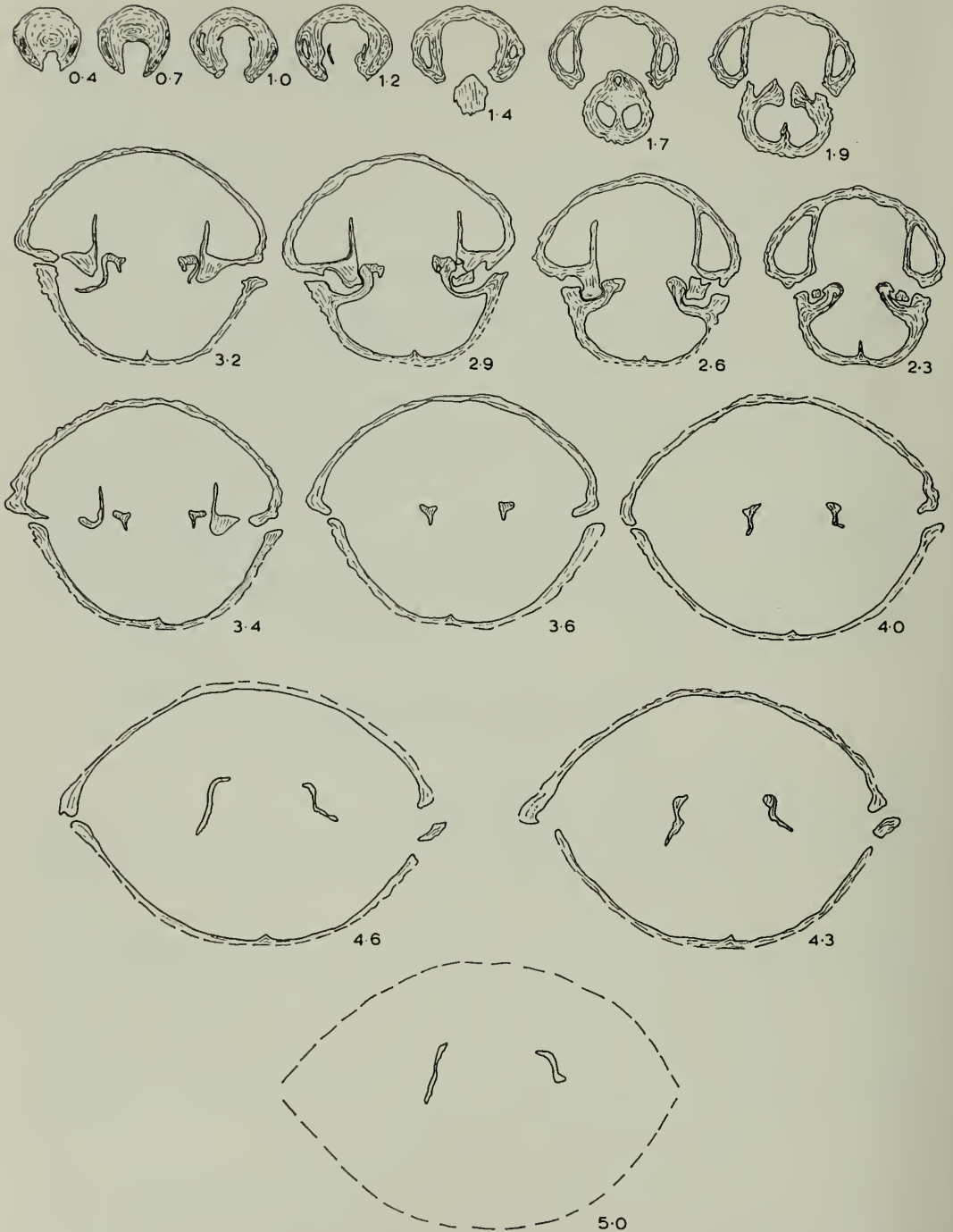


FIG. 24. Transverse serial sections of *A. (Acanthorhynchia) panacanthina* (Buckman & Walker). Topotype. Bajocian. Burton Bradstock, Dorset. Specimen donated by the B.M.(N.H.). ($\times 4$).

carefully prepared material. The ribs maintain a consistent spacing over the surface by constant dichotomy.

The shell is biconvex with the brachial valve the more inflated of the two. The beak is small and suberect. Disjunct trigonal deltidial plates flank the elliptical submesothyridid pedicle opening. Typically there are one or two well developed growth lamellae, although the "very numerous fine growth lines", noted by Buckman (1918) have not been observed on the material studied. The shell being very thin and delicate, short, slightly diverging dental lamellae and a short median septum are frequently seen, in pedicle and brachial valves respectively, of worn specimens.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.40 cm	0.68 cm	1.55 cm
3.05 cm	2.20 cm	3.53 cm
2.46 cm	1.73 cm	2.66 cm

Internal characters. Pedicle valve. The deltidial plates are only poorly developed, as seen externally, but in serial section they are seen to line the subquadrate delthyrial cavity laterally. Near the umbo, sections 1.0 to 1.2 in text-fig. 24 are seen two thin concave lamellae forming a weak pedicle collar. The dental lamellae are quite strong and parallel to one another, not breaking away from the ventral shell wall, as seen in serial section, until the teeth are fully inserted in their sockets; the lateral cavities are always relatively small.

Brachial valve. There is a long, low median septum. Septalial plates are not developed but there is a very distinctive thickening of the inner ends of the hinge plates, as shown in plate 12. This thickening possibly served for anchoring the diductor muscles. Lateral denticulae are present but, in common with the inner and outer socket ridges, are not well differentiated. The crura seem to be quite close to the shape described by Muir-Wood (1934) as *calcarifer*.

DISTRIBUTION. The author has not collected personally any material of this species and, therefore, it seems reasonable to quote the distribution given by Buckman and Walker (1889, p. 54) in their original description of the species: "This species appears to be confined to the district south of the Mendip Hills. It is a rare fossil, and it occurs only in the *parkinsoni* zone. It is, however, widely distributed, and has been obtained in Dorset, at Burton Bradstock, Broadwindsor, Clifton Maybank, Bradford Abbas, Halfway House and Combe Quarry near Sherbourne. In Somerset, at Misterton, Haselbury and at Crewkerne Station". The B.M.(N.H.) material, on which this revision is based, confirms this distribution. The species has not been recorded in the literature outside Britain and the only possible occurrence known to the author is represented by a few poorly preserved specimens collected by him from the *parkinsoni* zone of Normandy.

OCCURRENCE. No details were given by Buckman and Walker, but as the species seems to be restricted to the Inferior Oolite, it presumably lived in a fairly high-energy environment. The material in the collection of the B.M.(N.H.) shows quite

a wide range in the size of the individuals and as they are very well preserved this would indicate that they had not been carried far, if at all, before being buried.

A. (*Acanthorhynchia*) *spinulosa* (Oppel)

(Pl. 6, figs. 8-9, text-fig. 25 (top))

1850 *Hemithiris senticosa* (pars) Orbigny: 375.

1857 *Rhynchonella spinulosa* (pars) Oppel: 608.

1904 *Acanthothyris spinulosa* (Oppel); Loriol: 284-85, pl. 27, fig. 44.

1917 *Acanthothyris spinulosa* (Oppel); Rollier: 79.

EMENDED DIAGNOSIS. Medium sized *Acanthorhynchia*; transversely oval in outline; anterior commissure rectimarginate or with very slight uniplication; beak small and incurved; beak ridges and interarea present.

STRATIGRAPHICAL RANGE. Oxfordian—exact horizons not known.

TYPE SPECIMEN. A type specimen is not selected as this would have to be chosen from Orbigny's specimens of *Hemithiris spinulosa* (discussed below) and these are neither stratigraphically nor geographically accurately located.

MATERIAL. 2 specimens, collection of University of Dijon from Mt. Saon (Haute Marne) France; 6 specimens, collection of B.M.(N.H.) nos. B. 70044-49, from Haute Marne; 2 specimens Orbigny collection.

DESCRIPTION. *External characters.* The shell is equally biconvex and the width is greater than the length. The thin test is evenly covered with fine bifurcating ribs bearing numerous spine bases along their crests. The ribs are coarser and the spine bases more widely spaced than in *A. (Acanthorhynchia) panacanthina*.

Beak ridges are developed and limit the small but distinct interarea; the small, incurved beak is adpressed to the brachial valve and obscures the delthyrium. Deltidial plates are disjunct and only weakly developed; they appear briefly in a few of the anterior serial sections. Weakly developed growth lamellae, but not growth lines, may be present.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.30 cm	1.40 cm	2.54 cm
2.05 cm	1.10 cm	2.35 cm

Internal characters. Pedicle valve. Dental lamellae are completely lacking and the teeth are inserted laterally at a rather shallow angle.

Brachial valve. The most distinctive internal feature is the presence of what appears to be a cardinal process, developed from the inner hinge plates. The long, straight sockets, as seen in section 1.9 of text-fig. 25 appear to be distinctive. The crura are radulifer and curve slightly towards the pedicle valve. The median septum is poorly developed and is present only as a median ridge for most of its length.

DISTRIBUTION. The only records are from the Haute Marne area of France and from the Ledonien Jura.

REMARKS. The name *spinulosa* was first used by Oppel (1857) when he cited it as a "new name" for *Hemithiris senticosa* Orbigny in a list of Oxfordian fossils; unfortunately, he did not figure or state exactly what he meant by it.

Rollier (1917) suggested that the name *spinulosa* had been used by previous authors for two quite distinct species ; one of which he considered to be " Argovien "

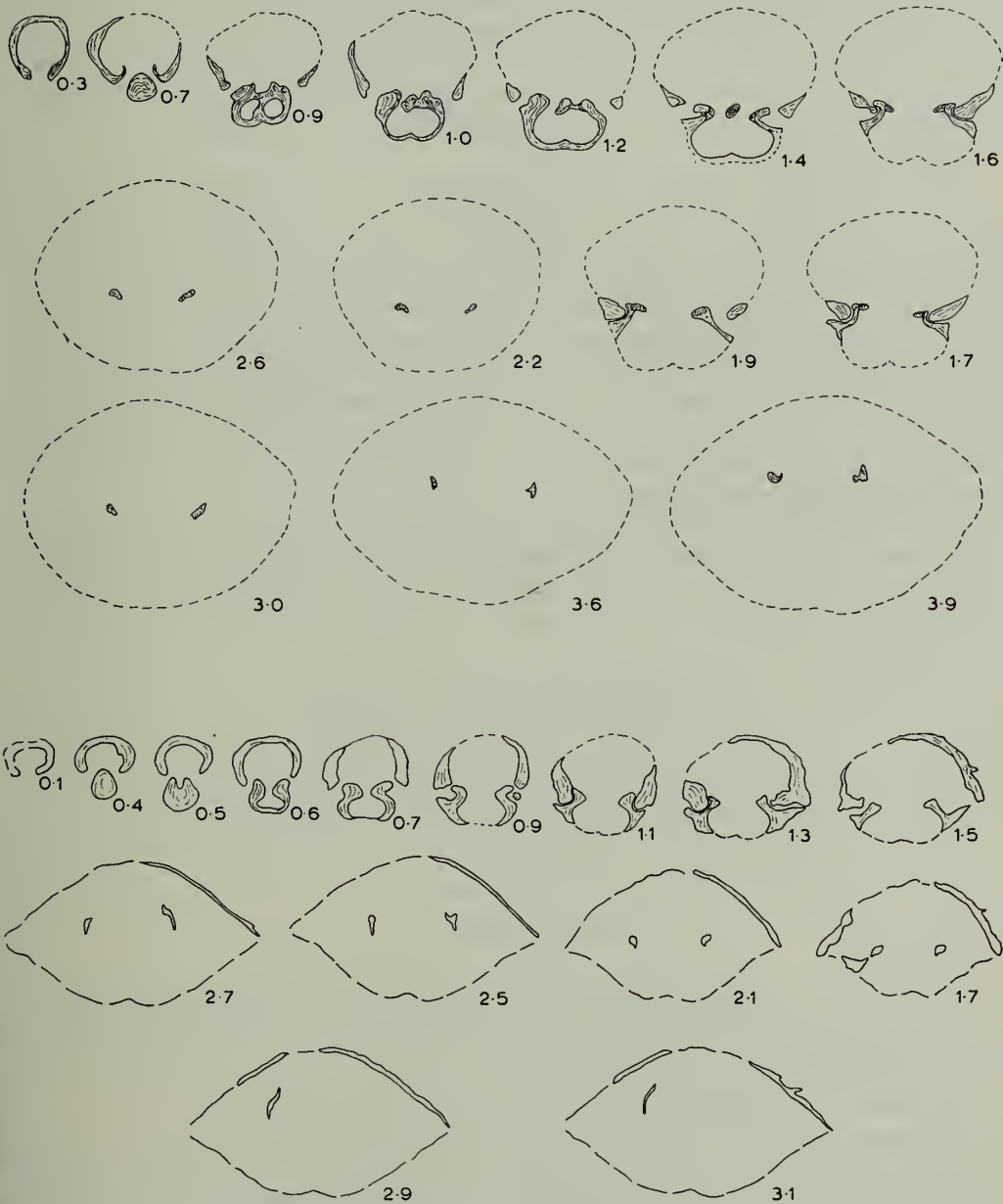


FIG. 25. TOP. Transverse serial sections of *A. (Acanthorhynchia) spinulosa* (Oppel). Oxfordian. Mont Saon, (Haute Marne), France. Specimen donated by the University of Dijon. ($\times 4$).
 BOTTOM. Transverse serial sections of *A. (Acanthorhynchia)* sp. Kimmeridgian. Oignon Limestone, (Ager & Evamy, 1963), Colomieu (Ain), France. ($\times 4$).

and the other "Oxfordien" in age. To remedy this he proposed that the name *spinulosa* be restricted to the larger, oval species from the "Argovien" and that the smaller, pyriform species of the "Oxfordien moyen et supérieur" be designated *Acanthothyris lorioli* sp. nov. Rollier's reason for preferring to restrict the name *spinulosa* to the larger form was that he considered Oppel's original designation inadequate and that, of the two species in question, this seemed to him to be the more likely to have been known to Orbigny, judging from the localities cited in the "Prodrome".

Plaster casts of the specimens labelled *Hemithiris senticosa* in the Orbigny collection at the Jardin des Plantes, Paris, were kindly made available to the author by the curator, Dr. Fischer. These specimens are in two boxes labelled 3782, containing three specimens from Chatel Censoir (Yonne) and 3782a, containing two specimens from Nantua (Ain). Both of the collection numbers contain a specimen of both *A. (Echinirhynchia) lorioli* and *A. (Acanthorhynchia) spinulosa* sensu Rollier. None of the specimens is referable to *A. senticosa* (Schlotheim). One of the specimens labelled 3782 probably belongs to a third, undescribed species and closely resembles a form collected by Dr. Evamy from the southern French Jura of Ain. Unfortunately not enough specimens of this form have been collected to make a full taxonomic investigation possible.

From the investigation of the original Orbigny material, described above, it seems that neither Oppel nor Rollier realised the diversity of specimens included by Orbigny under the name *Hemithiris senticosa*. However, the author would agree with Rollier's conclusions and these are here followed.

***A. (Acanthorhynchia) vilsensis* sp. n.**

(Pl. 6, figs. 10-12, text-fig. 26 (bottom))

1886 *Rhynchonella myriacantha* Deslongchamps; Rothpletz: 156, pl. 12, figs. 24-27.

NAME. From the type area of the "Vilser Alp" in the Tirol.

DIAGNOSIS. Medium sized *Acanthorhynchia* with rather coarse ribbing; beak suberect; uniplication in anterior commissure.

STRATIGRAPHICAL RANGE. Given by Rothpletz as Callovian—*macrocephalus* to *lamberti* zones.

TYPE SPECIMEN. The holotype designated is the specimen figured by Rothpletz (1886) pl. 12, fig. 25, which came from Legam bei Vils in the Tirol; this specimen is now in the Bayerische Staatsammlung für Paläontologie und historische Geologie in Munich, and is numbered AS xiv 2.

MATERIAL. 17 specimens from the Bayerische Staatsammlung.

DESCRIPTION. *External characters.* The adult specimens are biconvex, transversely oval in outline and with the width always greater than the length, while the juvenile forms have a subcircular outline. The beak is suberect; beak ridges and interarea are only very weakly developed. In nearly all the specimens examined, the beak had been broken off about level with the top of the brachial valve. In a few more complete specimens, the delthyrium appears to be open but this feature

has not been satisfactorily observed. The test is evenly covered with bifurcating, spine-bearing ribs which are quite coarse, as compared with other species in the genus. A few growth lamellae are frequently present but growth lines have only been observed on one specimen. The anterior commissure has a characteristic low uniplication.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.70 cm	1.00 cm	2.00 cm
1.53 cm	0.93 cm	1.67 cm
1.33 cm	0.70 cm	1.43 cm

Internal characters. The specimen sectioned, which appeared to be of typical preservation for the locality, was very badly recrystallized and with the shell almost completely missing. The effect of this has been to obliterate the fine structure together with the crura which were rapidly lost in a mosaic of crystalline calcite; the predominant lack of fine external ornament may also be a result of the poor preservation.

Pedicle valve. Slender, slightly diverging dental lamellae are present and bound a subquadrate delthyrial cavity. The teeth are large with distinctly flattened bases.

Brachial valve. The socket floors are very unusual in that they come to lie in a position sub-parallel to the plane of articulation. Both inner and outer socket ridges are well developed.

DISTRIBUTION. The species is only recorded from the type locality.

OCCURRENCE. In his original remarks, Rothpletz described it as occurring fairly abundantly in a "Brachiopoden-Lumachelle" together with numerous molluscs.

REMARKS. The species differs from *A. myriacantha*, as figured by Deslongchamps (1859), in being larger, having a uniplication in the anterior commissure and in having much coarser ribs on which the spine bases are more sparsely distributed. The small disjunct deltidial plates figured by Deslongchamps have not been observed in *A. (Acanthorhynchia) vilsensis*.

A. (Acanthorhynchia) sp.

(Pl. 7, figs. 10-11, text-fig. 25 (bottom))

MATERIAL. 4 specimens including B.M. BB.44168, BB.44169.

REMARKS. The material was collected from the thin bedded Oignon Limestone* (Ager and Evamy, 1963) near Colomieu (Ain). Both externally and internally, the species shows considerable resemblance to *A. (Acanthorhynchia) spinulosa*; however, the difference in stratigraphical horizon and the variability shown by the limited material available suggests that the species should be regarded as being derived from the former rather than conspecific with it. The largest specimen collected resembles one of the forms in the Orbigny Collection labelled *Hemithiris senticosa*.

* Oignon Limestone is of Upper Kimmeridgian age.

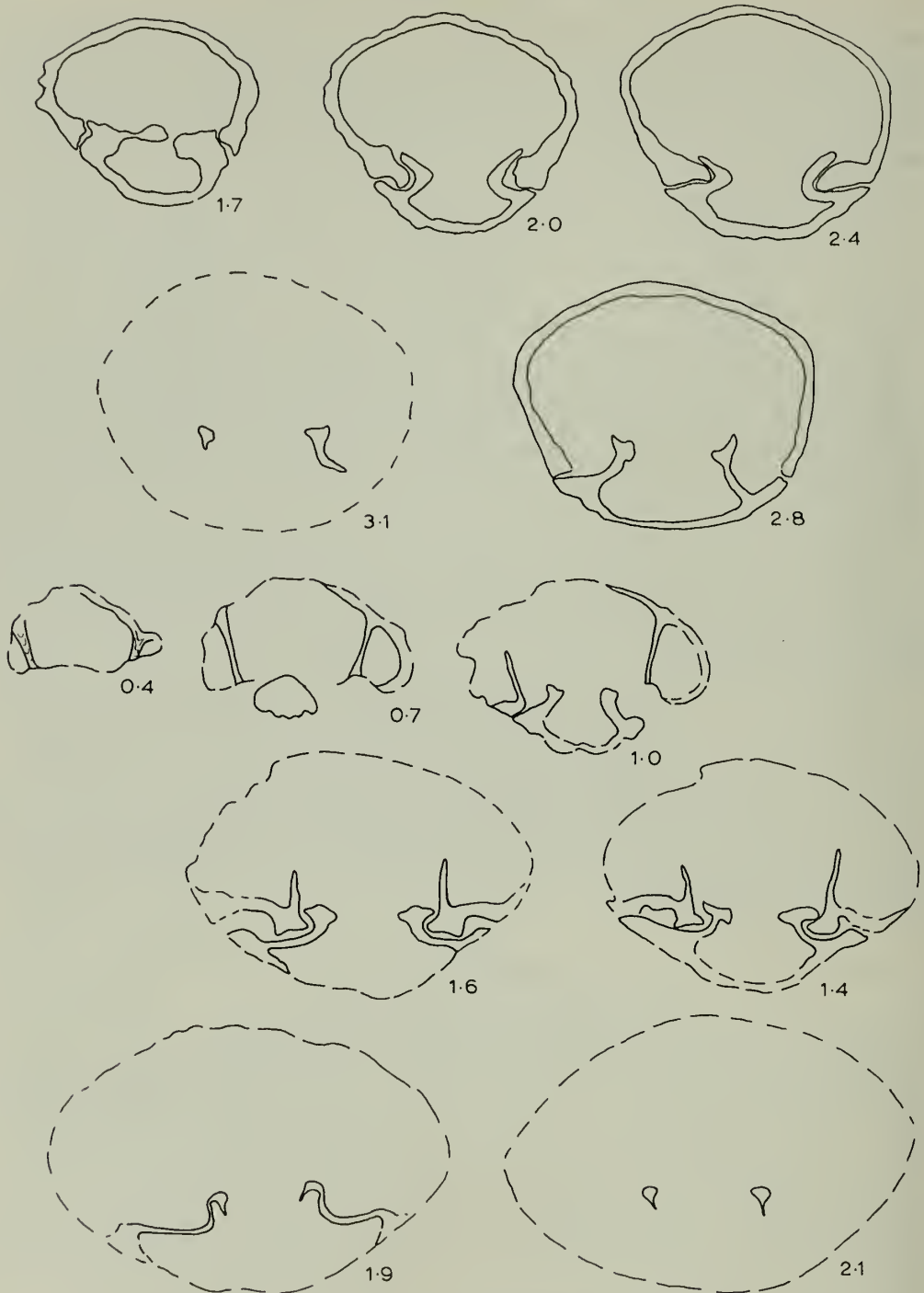


FIG. 26. TOP. Transverse serial sections of *A. (Echinirhynchia) senticosa* (Schlotheim). "Malm delta". Heiligenstadt, Germany. Specimen donated by the University of Erlangen. ($\times 8$). BOTTOM. Transverse serial sections of *A. (Acanthorhynchia) vilsensis* sp. nov. Topotype. Callovian. Legam bei Vils in the Tirol. Specimen donated by the Bayerische Staatsammlung. ($\times 8$).

ECHINIRHYNCHIA subgen. nov.

NAME. Latin echinus-im, the sea urchin : the shell of *Echinirhynchia* is covered with spines.

TYPE SPECIES. *Terebratulites senticosus* Schlotheim (1820).

DIAGNOSIS. Small to medium sized species of *Acanthorhynchia* ; usually sub-triangular in outline ; valves equally biconvex or with a flattened brachial and more inflated pedicle valve ; beak small and either adpressed to the brachial valve or suberect ; deltidial plates reduced or absent ; when the beak is suberect there is an open triangular delthyrium ; no dental lamellae or septalium ; anterior commissure rectimarginate.

STRATIGRAPHICAL RANGE. Oxfordian to Lower Volgian : *mariae*—*Gravesia* zones.

DISTRIBUTION. The subgenus appears, from the literature, to be restricted to the Jura, ranging from the southern French Jura through Switzerland to the Franconian Alb north of Erlangen ; the only records outside this area are of *A. (Echinirhynchia) fileyensis* (Buckman & Walker) from the Lower Calcareous Grit of Filey Brigg, Yorkshire, and of "*Acanthorhynchia* aff. *senticosus* (Schlotheim)" from Rumania (Patrulus, 1964).

REMARKS. The three species included are the only ones of which sufficient material has been obtained to allow description. Several nominal species, such as *Terebratula senticosus impressae* Quenstedt and *T. senticosus y alba* Quenstedt, almost certainly belong within the subgenus but the author has not been able to evaluate their position. The Quenstedt species mentioned above are the only ones recorded from the Swabian Alb area, although some of Opper's records of *Rhynchonella spinulosa* probably included material referable to *Echinirhynchia*.

A. (*Echinirhynchia*) *senticosus* (Schlotheim)

(Pl. 7, figs. 1-3, text-fig. 26 (top))

1820 *Terebratulites senticosus* Schlotheim: 268.

1834 *Terebratula senticosus* Buch: 59-60.

1838 *Terebratula senticosus* Buch: 162-63, pl. 16, fig. 5.

1858 *Terebratula senticosus* Quenstedt: 457.

1871 *Terebratula senticosus silicea* Quenstedt: 115, pl. 39, fig. 66.

1886 *Rhynchonella senticosus* (Schlotheim); Rothpletz: 93, 156-57, pl. 15, figs. 4-9.

1889 *Acanthothyris senticosus* (Schlotheim); Buckman and Walker, 55-56.

1917 *Acanthothyris senticosus* (Schlotheim); Rollier: 80.

1918 *Acanthorhynchia senticosus* (Buch); Buckman, 70.

EMENDED DIAGNOSIS. Small to medium sized, pyriform *Echinirhynchia* ; test covered with numerous fine, spinose ribs ; beak relatively large and suberect to erect ; deltidial plates absent resulting in an open triangular delthyrium ; recti-marginate.

STRATIGRAPHICAL RANGE. Kimmeridgian—Lower Volgian : *pseudomutabilis* to *Gravesia* zones.

TYPE SPECIMEN. Neotype (pl. 7, fig. 1), here designated, is the specimen figured by Rothpletz (1886) pl. 15, fig. 5, which is No. AS vii 330 in the collection of the Bayerische Staatsammlung für Paläontologie und historische Geologie in Munich. It is considered desirable to designate a neotype as the name *sentica* has been used very loosely in the past for widely differing forms.

MATERIAL. 12 specimens from the collection of the University of Erlangen ; 11 specimens from the Bayerische Staatsammlung, Munich.

DESCRIPTION. *External characters.* The following is a translation of the original description by Schlotheim, "Partly in very complete examples, with perfectly preserved shells, from Grumbach, near Amberg, in the Pfalz, petrified in chert and probably belonging to the Jura formation. This very rare and remarkable Terebratulite, only recently discovered, has a somewhat elliptical, almost pear-shaped form, it is not particularly thick, is regularly convex with a fine, evenly striated, shagreen like surface and on both valves the somewhat prominent rays are covered with numerous, small sharp spines, by which this and *spinus* may be distinguished from all other known species. It is very seldom found".

The Schlotheim description is quite accurate and mentions the two most distinctive characters, namely the pyriform shape and the fine, spine-covered ribs. The ribs characteristically bifurcate laterally thereby maintaining an even distribution over the surface. The species is also characterized by the possession of a rectimarginate anterior commissure. The beak is suberect and does not obscure the triangular delthyrial opening ; no deltidial plates have been observed. Beak ridges and inter-area are not developed. Some specimens have a few growth lamellae developed, but growth lines are not present ; it is possible that the latter may have been obliterated as a result of the silicification suffered by all the specimens examined. The valves are about equally biconvex, although the brachial valve tends to be rather flat and may be the less inflated.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.35 cm	0.61 cm	1.17 cm
1.94 cm	0.87 cm	1.62 cm
1.35 cm	0.67 cm	1.22 cm

The last set of figures are the dimensions of the neotype.

Internal characters. The specimen sectioned was from Heiligenstadt, Franconia, and had a silicified shell and dolomitised infilling. This preservation has resulted in the loss of all fine detail and it has only been possible to give rather generalized drawings of the internal structures.

Pedicle valve. There are no dental lamellae and the large teeth are inserted laterally at a shallow angle.

Brachial valve. A cardinal process is present. Inner and outer socket ridges are both well developed. The form of the crura could not be determined as they disappeared into the recrystallized matrix immediately below the last section shown in text-fig. 26—top.

DISTRIBUTION. The Franconian and Swabian Jura.

OCCURRENCE. Dr. Zeiss, of Erlangen, has stated (personal communication 1965) that the material from Heiligenstadt occurs in the "Schwammfacies". There is no information available concerning the material figured by Rothpletz (1886).

REMARKS. The species, as remarked by Schlotheim, is rare and this has probably been the cause of the confusion about which species the name *senticosa* should be applied to. However, the silicified specimens figured by Rothpletz from the original locality cited by Schlotheim seem to fit the latter's description so exactly that there seems no doubt that this was the species intended by him. As can be seen from the original description, no exact geological horizon was given and some of the difficulty has undoubtedly arisen through Buch (1838) citing the Schlotheim locality for his *Terebratula senticosa* and stating the horizon for this locality to be "Dans les couches jurassiques inférieures, au-dessus du Lias". This statement seems to have lead several authors to reject the name *senticosa* when describing Upper Jurassic forms as they assumed Schlotheim's species was from the Middle Jurassic. However, Rothpletz gives the topotype material as being "Malm epsilon" in age and this agrees with the age given by Quenstedt (1871) for his *Terebratula senticosa silicea* from Sirchingen, while the material from Heiligenstadt in the collection of University of Erlangen is from the "Malm delta".

A. (*Echinirhynchia*) *lorioli* (Rollier)

(Pl. 7, figs. 7-9, text-fig. 27)

- 1850 *Hemithiris senticosa* (pars) Orbigny: 375.
 1857 *Rhynchonella spinulosa* (pars) Opperl: 608.
 1871 ?*Terebratula y alba* Quenstedt: 114, pl. 39, figs. 63-65.
 1897 *Acanthothyris spinulosa* (Opperl); Loriol: 146, pl. 17, fig. 17.
 1904 *Acanthothyris spinulosa* (Opperl); Loriol: 284-85, pl. 27, fig. 45.
 1917 *Acanthothyris Lorioli* Rollier: 79.
 1917 ?*Acanthothyris dealbata* Rollier: 80.

EMENDED DIAGNOSIS. Medium sized, pyriform or sub-circular *Echinirhynchia*. Biconvex; rectimarginate; beak adpressed to the brachial valve.

STRATIGRAPHICAL RANGE. Oxfordian—the only exact records are from the *transversarium* zone.

TYPE SPECIMEN. Lectotype, here selected, the original specimen figured by Loriol (1897) pl. 17, fig. 17, collected from Montfaucon (Jura bernois).

MATERIAL. 7 specimens from the collection of the B.M.(N.H.) two, BB.44166, BB.44167, from the Jura; 10 specimens collected by Dr. Enay from the central French Jura; 2 specimens collected by Dr. Evamy from Ain.

DESCRIPTION. *External characters.* The species is normally biconvex but some specimens show a flattened brachial valve. The test is covered with many fine, bifurcating ribs bearing numerous fine spines. The beak is small and closely pressed to the brachial valve, obscuring the delthyrium; beak ridges and interarea not developed. Growth lamellae are sometimes present but growth lines have not been observed.

DIMENSIONS OF FIGURED SPECIMEN.

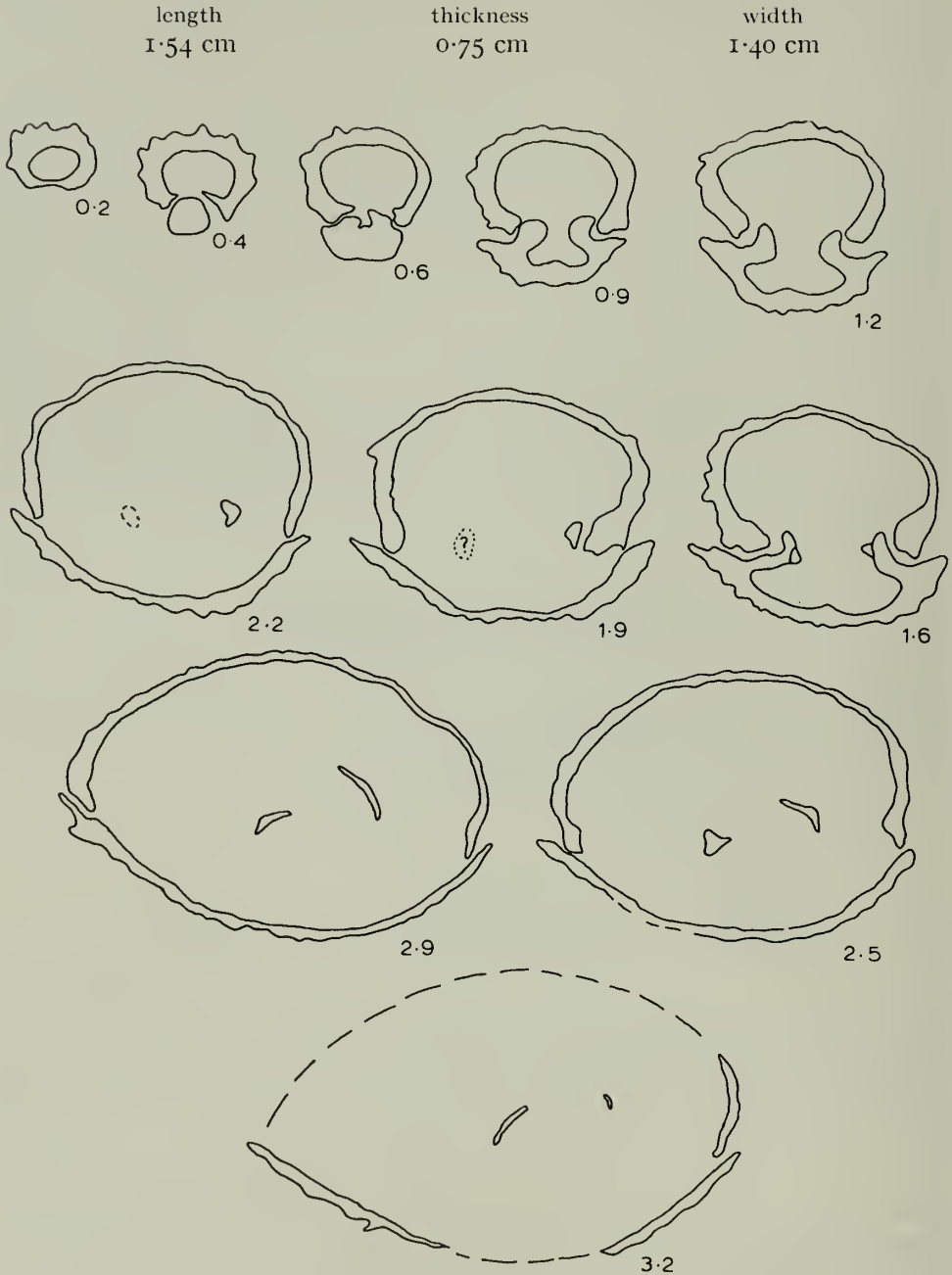


FIG. 27. Transverse serial sections of *A. (Echinirhynchia) lorioli* (Rollier). Oxfordian—*transversarium* zone. St. Sorlin, Liefnans (Jura), France. ($\times 8$).

Internal characters. Pedicle valve. There are no dental lamellae. The deltidial plates are disjunct and only weakly developed. The teeth are strong and inserted laterally at a rather shallow angle.

Brachial valve. A cardinal process is not present but the species exhibits the thickened inner hinge plates characteristic of the genus. The crura were not well preserved but are possibly of the calcarifer type. A median septum is only present as a low ridge.

DISTRIBUTION. The species has only been definitely recorded from the central and southern French Jura.

OCCURRENCE. The material collected by Dr. Enay was obtained from dark-coloured clays where it was associated with *Monticlarrella triloboides*.

REMARKS. The specimen sectioned came from St. Sorlin (Jura) one of the localities mentioned by Rollier in his original description.

The separation of *A. (Echinirhynchia) lorioli* from *A. (Acanthorhynchia) spinulosa* is described under the latter.

***A. (Echinirhynchia) fileyensis* (Buckman & Walker)**

(Pl. 7, figs. 4-6)

1889 *Acanthothyris senticosa* var. *fileyensis* Buckman and Walker: p. 56.

EMENDED DIAGNOSIS. Small to medium sized *Echinirhynchia*; beak small and suberect to erect; valves equally biconvex.

STRATIGRAPHICAL RANGE. Oxfordian—*mariae* and lower *cordatum* zones.

TYPE SPECIMEN. Lectotype, here selected, specimen no. B. 31867 in the Walker Collection of the B.M.(N.H.), collected from the Lower Calcareous Grit of Filey, Yorkshire.

MATERIAL. 6 specimens from the Walker Collection in the B.M.(N.H.); nos. B. 31313, B. 31335, B. 31275; 2 specimens from the collection of the Naturhistorisches Museum, Basel.

DESCRIPTION. *External characters.* The shell is biconvex and pyriform in outline with a straight anterior margin. The ribs are fine but well marked and covered with spine bases. The beak is small and erect or sub-erect; beak ridges and inter-area are not developed. Details of deltidial plates, if any, and delthyrium not observed.

DIMENSIONS OF FIGURED SPECIMEN. The following measurements are those of the lectotype.

length	thickness	width
0.80 cm	0.37 cm	0.74 cm

Internal characters. Not investigated through lack of material.

DISTRIBUTION AND OCCURRENCE. The species has only been definitely recorded from Filey, Yorkshire, where it occurs in the Lower Calcareous Grit. The only other possible conspecific material known to the author is two specimens from the "Renggeri-Thon" of Baden, in the collection of the Naturhistorisches Museum, Basel and numbered L 1701/1-2.

REMARKS. The form was first mentioned by Buckman and Walker in 1889 in their discussion of the spinose Rhynchonellidae, when they described it under the name of *Acanthothyris senticosa* var. *fileyensis* and suggested that it resembled *A. senticosa* of Orbigny. However, as *A. (Echinirhynchia) fileyensis* shows marked differences from both the specimens in the Orbigny Collection and *A. (Echinirhynchia) senticosa* (Schlotheim), it has been decided to describe it as separate species despite the paucity of material.

Subfamily **TETRARHYNCHIINAE** Ager, 1965b
Genus **SOMALIRHYNCHIA** Weir

- 1925 *Somalirhynchia* Weir: 79.
1929 *Somalirhynchia* Weir; Weir: 38-39.
1935 *Somalirhynchia* Weir; Muir-Wood: 93.
1964 *Praecyclothyris* Makridin, 150-51.
1965b *Somalirhynchia* Weir; Ager: H614.

TYPE SPECIES. *S. africana* Weir, by original designation.

EMENDED DIAGNOSIS. Large, subpentagonal, trilobate rhynchonellids; 20-30 coarse, simple, subangular ribs; large, sub-erect beak; possesses septalial plates and median septum, which together form a septalium; crura radulifer.

STRATIGRAPHICAL RANGE. Upper Oxfordian—Lower Kimmeridgian.

DISTRIBUTION. Somaliland, Syria, N.W. Europe, Russia.

REMARKS. Weir (1925, 1929) gave the name *S. africana* to the species figured by Noetling (1886) as *Rhynchonella moravica* Uhlig; he suggested that the differences in outline and particularly in muscle scar patterns necessitated regarding *R. moravica* Noetling as differing from *R. moravica* Uhlig not only specifically but generically. The author considers that Weir was probably correct in establishing a new species for Noetling's *R. moravica*. However, in internal structure, as well as general external appearance, *S. africana*, in the author's opinion, closely resembles *R. moravica* Uhlig and should be regarded as congeneric with it.

In basing his taxonomy almost entirely on the muscle scar patterns, Weir was closely following the ideas of Buckman. However, it is now considered that the similarity exhibited by all the other features outweigh in taxonomic significance the dissimilarity of the muscle patterns. The internal details of *R. moravica* Uhlig were figured by Wiśniewska (1932) and, allowing for the differences in appearance caused by her angle of sectioning, are closely comparable to those given by Muir-Wood (1935) for *S. africana*. They appear to have little in common with *Septaliphoria arduennensis* (Oppel), the type species of *Septaliphoria* Leidhold, to which genus *R. moravica* Uhlig was assigned by Wiśniewska. Consequently, the author does not understand on what grounds Muir-Wood (1935) remarked, "Further study of the internal characters of *R. moravica* by Wiśniewska (1932, p. 22) has emphasized the differences between the two species (i.e. *R. moravica* Uhlig and *S. africana* Weir). *R. moravica* is now assigned to the genus *Septaliphoria* (Leidhold 1920)".

The wide geographical distribution of the genus is coupled with a very limited stratigraphical range. It is considered that the distribution of the genus can be

extended to Russia, as it appears from Makridin's figures that some at least of his species of the genus *Praecyclothyris* should be attributed to *Somalirhynchia*. That the genus has not previously been recorded from Europe is probably the result of its name, which has possibly been taken by previous authors as implying a restricted geographical occurrence.

Somalirhynchia sutherlandi (Davidson)

(Pl. 7, figs. 12-16, text-fig. 29)

- 1873 *Rhynchonella Sutherlandi* Davidson: 196, pl. 8, figs. 1-2.
 1878 *Rhynchonella Sutherlandi* Davidson; Davidson: 190-91, pl. 25, figs. 5-8.
 1917 *Rhynchonella Sutherlandiae* Davidson; Rollier: 172.
 1918 *Rhynchonella Sutherlandi* Davidson; Buckman: 51.

EMENDED DIAGNOSIS. Medium to large sized *Somalirhynchia*; 15-25 coarse, simple, angular ribs; usually trilobate; suberect beak, septalium present; crura radulifer.

STRATIGRAPHICAL RANGE. Kimmeridgian—probably restricted to the upper *mutabilis* and *pseudomutabilis* zones.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Davidson (1878), pl. 25, fig. 5).

MATERIAL. 19 specimens from the collection of the Geological Survey of Scotland, together with the very limited material available at the B.M.(N.H.) nos. B. 29749, B. 29752, B. 22586, B. 29751, B. 29753. A recent attempt by the author to collect further material yielded a single fragmentary specimen.

DESCRIPTION. *External characters.* The species is distinctive on account of the very large size attained by many individuals; Davidson (1878) claimed it to be the largest Mesozoic rhynchonellid. The outline is subpentagonal and the shell is biconvex with the brachial valve the more inflated. It is generally trilobate but a few specimens have been observed displaying quite marked asymmetry. Width, according to Davidson, is always greater than length, and while this seems to be correct the crushed nature of much of the material makes this difficult to ascertain in more than a few cases. Plate 7 figures the best preserved material available.

The strong, suberect beak is flanked by well defined beak ridges which limit the incurved interarea. A relatively small pedicle opening is present; the deltidial plates, as seen in transverse section, are strongly conjunct. Fine, concentric growth lines have been observed on one specimen; this may well reflect the poor preservation rather than the genuine lack of such ornament on most specimens.

DIMENSIONS OF FIGURED SPECIMEN.

length	thickness	width
2.67 cm	2.33 cm	3.16 cm

Internal characters. The specimen sectioned was slightly crushed, resulting in dorso-ventral flattening of the shell. The outline of some of the internal features was partly distorted by pressure solution caused by the coarse, quartz matrix.

Pedicle valve. A pedicle collar is present; the deltidial plates are conjunct and "crumple up" against one another. A quadrate delthyrial cavity is flanked by

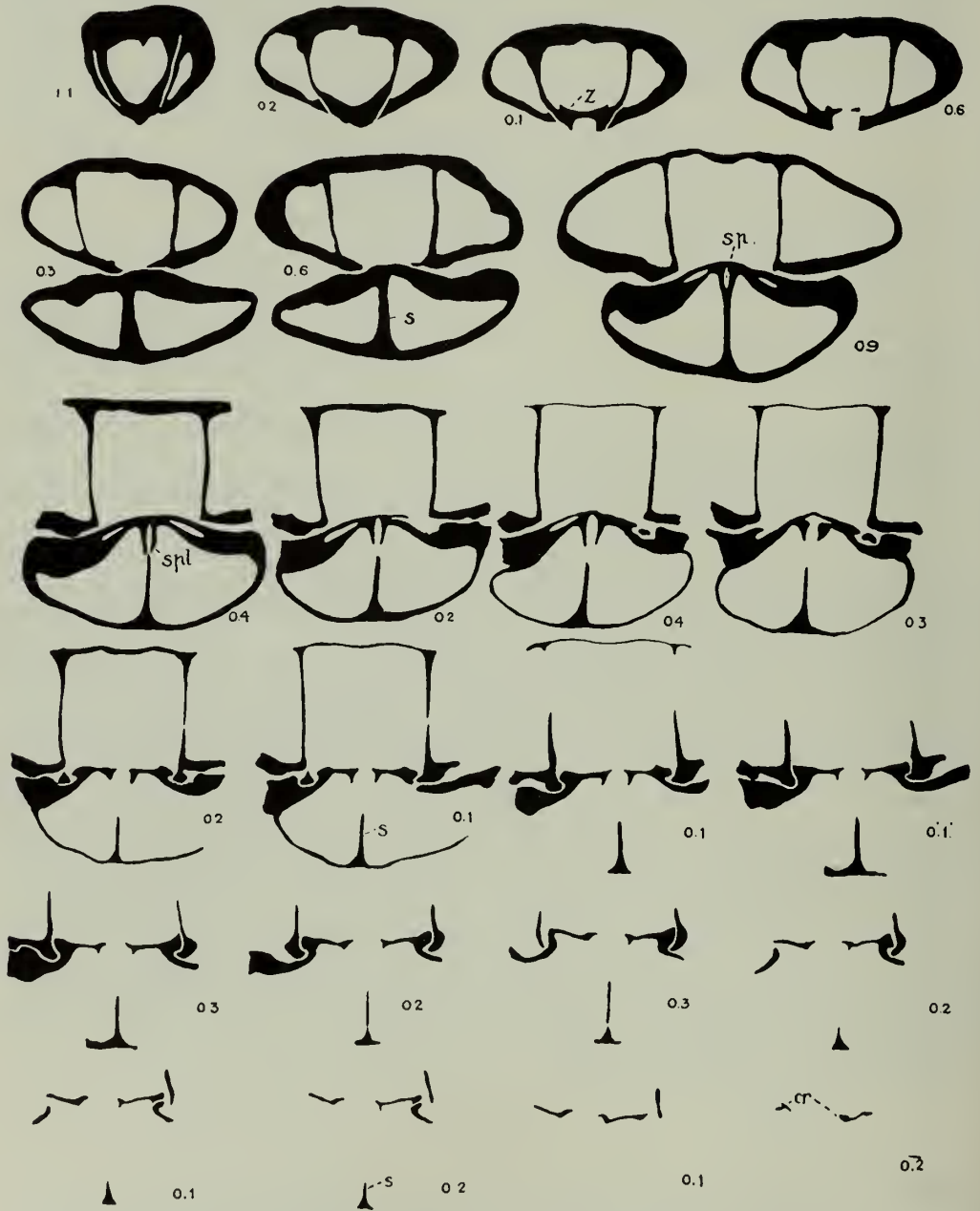


FIG. 28. Transverse serial sections of *Somalirhynchia africana* Weir. Taken from Muir-Wood (1935, fig. 8, p. 95).

long, stout, subparallel dental lamellae. The hinge apparatus is strongly developed with massive crenulated teeth and strong lateral denticulae.

Brachial valve. The most obvious feature is the presence of a median septum and well developed septalial plates forming a septalium. The crural bases do not become apparent, as seen in transverse section, until after the hinge plates have divided and the septalial plates disappeared. The crura are radulifer. The sockets are crenulated and both the inner and outer socket ridges are strongly developed.

DISTRIBUTION. The species has only been recorded from the Helmsdale area of Sutherland, Scotland.

OCCURRENCE. The only known occurrence is in the Kimmeridgian "Boulder Beds" of the Helmsdale area, east Sutherland, Scotland. Bailey and Weir (1935) suggested that the rhynchonellids, together with the terebratulids and corals, owed their presence in these beds to the effects of submarine faulting. They suggested a near-shore fault scarp which, "separated a comparatively shallow-water facies, characterized by rounded pebbles, sand, *Rhynchonella*, *Terebratula*, *Ostrea*, sea urchins corals, etc. from a comparatively deepwater facies, characterized by mud, debris of land plants, ammonites etc.". The rhynchonellids etc. were then swept over the scarp edge by the movements of the fault and the accompanying tsunamis.

Ager (1965a), accepting this hypothesis, suggested that the *S. sutherlandi* inhabited, "sublittoral, non-depositional sea floors"; the rarity of the species then being accounted for by the infrequency with which such deposits are preserved. However, although no other representative of the genus occurs in Britain, *S. moeschi* (Haas) is present in the "Rauracian" of the French and Swiss Jura. Material of the latter species has been given to the author by Dr. Enay of the University of Lyon and he has stated (personal communication, 1965), that *S. moeschi*, at least within the Jura meridionale, always occurs in association with corals. From this it would also seem possible that *S. sutherlandi* inhabited shallow marine environments and was not necessarily restricted to rocky shores. The presence of corals at Helmsdale indicates the possibility of a reef environment being available.

REMARKS. It appears that *S. sutherlandi* has not been further described since Davidson in 1878 and during this time there have been only two tentative generic assignments. In the first, Buckman (1918), placed it in his genus *Rhactorhynchia* but although he indicated his uncertainty he did not discuss the matter. Ager (1965a), suggested the possibility of *sutherlandi* being in the genus *Russirhynchia* Buckman, which is otherwise restricted to the Russian Platform. The present author, however, prefers to attribute the species to the genus *Somalirhynchia* Weir. Reproduced below, text-figure 28, are the serial sections given by Muir-Wood (1935) for the type species, *S. africana* Weir, and it can be seen that they show a striking resemblance to those of *S. sutherlandi*. Externally the species are also comparable in general shape, ribbing, and form of the beak and the pedicle opening. Both internally and externally "*R.*" *sutherlandi* appears to be much closer to *S. africana* than to the type species of *Russirhynchia* namely, *R. fischeri* (Rouillier).

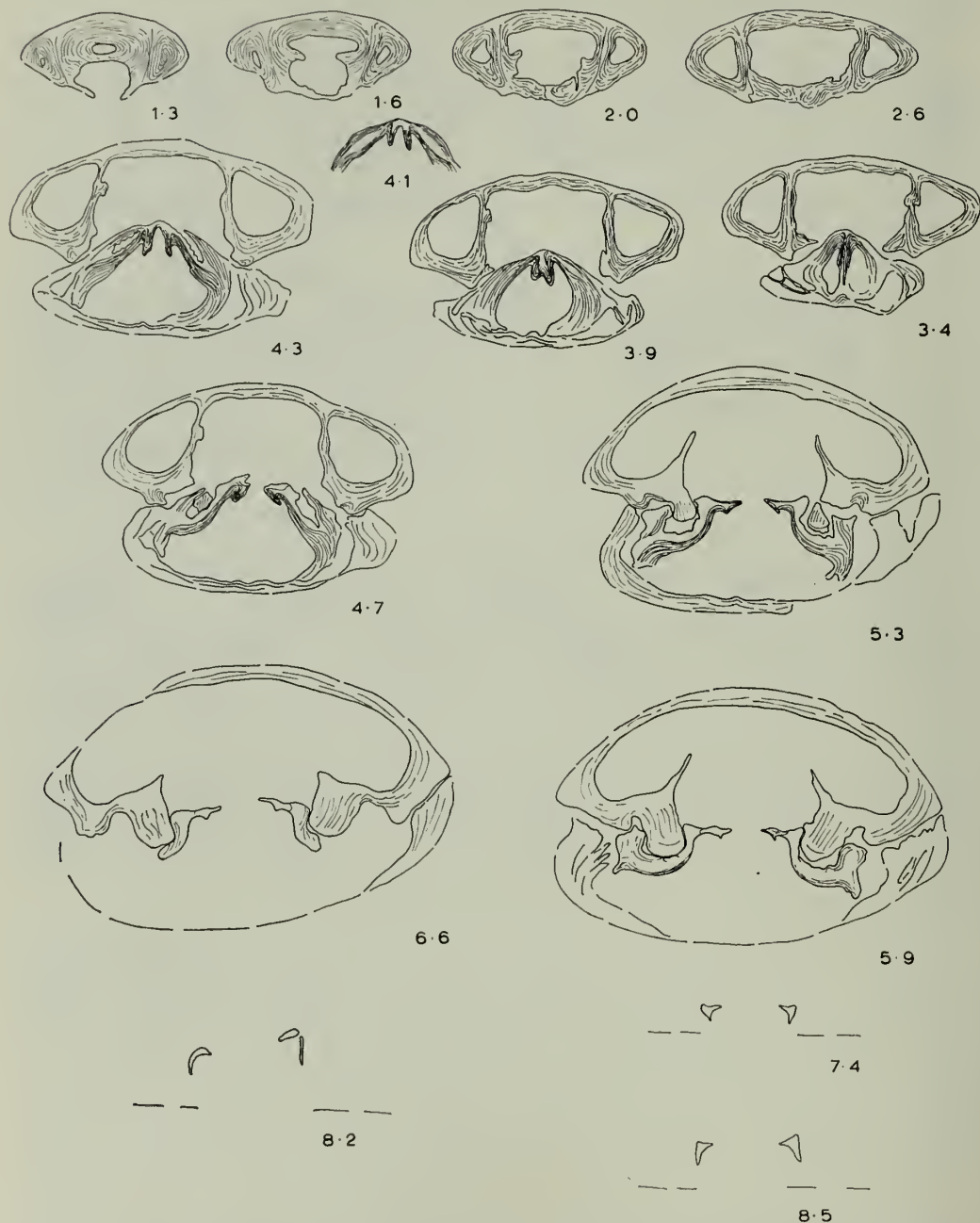


FIG. 29. Transverse serial sections of *Somalirhynchia sutherlandi* (Davidson). Topotype. Kimmeridgian. Boulder Beds. West Garty, Sutherland. Specimen donated by the Geological Survey, Edinburgh. ($\times 3$).

Somalirhynchia moeschi (Haas)

(Pl. 8, figs. 1-3, text-fig. 30)

1890 *Rhynchonella trilobata* Zieten var. *Möschii* Haas: 58-59, pl. 7, fig. 7, pl. 8, figs. 1-2.1893 *Rhynchonella trilobata* Zieten var. *Moeschi* Greppin: 98, pl. 7, figs. 3-4.1917 *Rhynchonella Moeschi* Rollier: 174.1932 ?*Septaliphoria moravica* (Uhlig); Wiśniewska: 22-24, pl. 5, figs. 3-4.1964 *Praecyclothyris moeschi* (Rollier); Makridin: 158-60, pl. 6, fig. 8, pl. 7, fig. 1.

EMENDED DIAGNOSIS. Medium to large, subpentagonal *Somalirhynchia*; markedly trilobate with about 6-8 ribs on the fold; septalium present although septalial plates relatively weakly developed; crura radulifer.

STRATIGRAPHICAL RANGE. Upper Oxfordian; records, such as those of Haas (1890), from the Kimmeridgian are almost certainly the result of misidentifying *Lacunosella trilobataeformis* Wiśniewska. The latter species strongly resembles *S. moeschi* externally but can be readily differentiated by its possession of bifurcating ribs.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Haas (1890) pl. 7, fig. 1; the specimen was obtained from the "Wangener Schichten" of "Engelberg bei Olten".

MATERIAL. 80 specimens collected by Dr. Enay from the "départements" of Jura and Ain. 6 specimens from the collection of the University of Dijon labelled, "Corallien inférieur?", 7 specimens collected by the author from Pontarlier, near Besançon.

DESCRIPTION. *External characters.* The species has a subpentagonal outline and is markedly trilobate. There are between 20 and 30 coarse, simple subangular ribs of which 6 to 8 lie on the fold.

The sharp, suberect beak is flanked by weak beak ridges and these in turn delimit the slightly incurved interarea. The deltidial plates, which tend to project slightly around the circular, submesothyridid pedicle opening, are conjunct; however, in many specimens the deltidial plates are missing, presumably through having fallen out after death, leaving an open delthyrium.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3.57 cm	2.70 cm	3.82 cm
3.12 cm	2.18 cm	3.00 cm

Internal characters. Pedicle valve. The lateral cavities are small and limited by slender, subparallel, persistent dental lamellae. The delthyrial cavity is quadrate. The teeth are crenulated; lateral denticulae are only weakly developed.

Brachial valve. A septalium is present; although the median septum is quite strong and persistent, the septalial plates are only weakly developed. The radulifer crura have clearly differentiated crural bases. The hinge plates are arched ventrally.

DISTRIBUTION. The French and Swiss Jura; ? Poland.

OCCURRENCE. The specimens collected by the author came from a limestone with a typical reef fauna, namely lamellibranchs, terebratulids, gasteropods and



FIG. 30. Transverse serial sections of *Somalirhynchia moeschi* (Haas). Oxfordian—*transversarium* zone. Arinthod (Jura). ($\times 3$).

echinoids together with numerous branching corals. *S. moeschi* was the most common brachiopod, followed in numbers by the smooth terebratulids, while the ribbed terebratulids were the rarest element of the fauna.

REMARKS. In discussing *Septaliphoria moravica* (Uhlig), Wiśniewska suggested that *Rhynchonella trilobata* var. *Möschii* was probably a synonym. Unfortunately, the author has not seen the original specimens of Uhlig, Haas or Wiśniewska. Judging from the published figures and assuming these to be typical, it would appear that the specimens described by Wiśniewska are conspecific with *S. moeschi* (Haas) and that "*Rhynchonella*" *moravica* Uhlig is probably a separate species, the latter being differentiated by its more trilobate form. However, "*R.*" *moravica*, which occurs in the *bimammatum* zone is almost certainly congeneric.

In 1964, Makridin divided *R. moeschi* Rollier into two subspecies, namely *moeschi moeschi* and *moeschi donetziana*. He then selected the latter as the type of his new genus *Praecyclothyris*; however, as under the international rules of nomenclature the type must be *moeschi moeschi*; it is suggested that *Praecyclothyris* is a synonym of *Somalirhynchia* Weir. As *Somalirhynchia* is not mentioned in the Russian "Treatise", it is assumed that the rather obscure publications in which it has been described are not known to palaeontologists in the Soviet Union.

Subfamily CYCLOTHYRIDINAE Makridin, 1955

Genus *SEPTALIPHORIA* Leidhold

- 1920 *Septaliphoria* Leidhold: 354-55.
 1932 *Septaliphoria* Leidhold; Wiśniewska: 18-20.
 1960 *Septaliphoria* Leidhold; Makridin: 251-52.
 1964 *Septaliphoria* Leidhold; Makridin: 96-7.
 1965b *Septaliphoria* Leidhold; Ager: H619.

TYPE SPECIES. *Rhynchonella arduennensis* Opper, by original designation.

EMENDED DIAGNOSIS. Medium sized, subpentagonal rhynchonellids; 10-25 coarse, simple, subangular ribs; septalium present; crura radulifer.

STRATIGRAPHICAL RANGE. Oxfordian—?Kimmeridgian.

DESCRIPTION. *External characters.* The genus consists of ordinary looking uniplicate rhynchonellids, having a tendency towards asymmetrical development of the anterior commissure. The complete, bilobed asymmetry characteristic of *Torquirhynchia* is very rarely found and in most cases the asymmetry of the anterior commissure has resulted from displacement of the uniplication. *Septaliphoria* is biconvex with the brachial valve the more inflated; there is no posterior smooth area.

The well developed, suberect beak is flanked by beak ridges which limit an incurved interarea. A large, hypothyriddid or submesothyriddid pedicle opening is present; the deltidial plates are usually, but not invariably, conjunct.

Internal characters. Pedicle valve. The dental lamellae are subparallel and relatively short. The teeth may be slightly crenulated; lateral denticulae are variably developed.

Brachial valve. The most important feature is the septalium ; in his original description Leidhold (1920) regarded this structure as the diagnostic feature of the genus.

The crural bases are clearly differentiated and are distinctive in that they can be seen at the same level as the septalial plates in transverse section. In both the species sectioned, the crura ended with the curiously shaped, but consistent, processes seen in text-figs. 31-33.

SPECIES. The following nominal species are attributed to the genus :

S. arduennensis (Oppel) (1858, pp. 615, 639, 654)

?*S. hudlestoni* (Rollier) (1917, p. 172)

S. paucicosta sp. nov.

S. pinguis (Roemer) (pars in Wiśniewska 1932, pp. 24-29, pl. I, figs. 1-18)

?*S. septentrionalis* sp. n.

?*S. pectunculoides* (Etallon) (in Makridin 1964, pp. 102-5, pl. I, figs. 4-6)

S. sobolevi Makridin (1964, pp. 97-99, pl. I, figs. 16-18).

DISTRIBUTION. The taxonomic confusion which has surrounded the genus, together with the lack of published serial sections, makes identification from the literature very difficult. However, the genus occurs in Yorkshire, northern France, the Swiss Jura and ?Dorset. Some of Makridin's species of *Septaliphoria* from the Russian Platform also undoubtedly belong to the genus, as here defined.

REMARKS. Much confusion has arisen about the exact nature of the genus, mainly as a result of two factors. Firstly, Leidhold (1920) chose as his type species the poorly defined *Rhynchonella arduennensis* of Oppel, and secondly, because Leidhold's description of the septalium was based on a misunderstanding regarding its development.

The synonymy of the type species is described under *S. arduennensis*. A full description, with figures and sections of the septalium has already been given in the section on morphology and it is only necessary to repeat here that it forms through the fusion of the septalial plates with the septum and not as a result of a bifurcation of the septum, as originally suggested by Leidhold.

***Septaliphoria arduennensis* (Oppel)**

(Pl. 8, figs. 4-5, text-figs. 31-32)

1858 *Rhynchonella Arduennensis* Oppel: 615, 639, 654.

1871 *Tevebratula inconstans* Quenstedt: 141, pl. 40, fig. 57.

1917 *Rhynchonella Arduennensis* Oppel; Rollier: 171-72.

1920 *Septaliphoria arduennensis* (Oppel); Leidhold: 354, pl. 5, fig. 2.

1932 *Septaliphoria arduennensis* (Oppel); Wiśniewska: 18.

EMENDED DIAGNOSIS. Medium sized subpentagonal to subtriangular *Septaliphoria* ; biconvex ; frequently slightly asymmetrical ; about 20 simple, subangular ribs ; well developed septalium crura radulifer.

STRATIGRAPHICAL RANGE. Lower Oxfordian ; *cordatum* and lower *transversarium* zones.

TYPE SPECIMEN. A neotype is here proposed in view of the uncertainty which has surrounded this important species. Although the specimen chosen is not from any of the localities cited by Oppel (1858) it is from the horizon mentioned by him, namely the "Terrain à Chailles", and has been selected to conform as nearly as possible to the specimen figured by Leidhold, as he was the first to figure the species as such and, consequently, his figure has been accepted as definitive both of the species and of the genus *Septaliphoria* of which it is the type. Unfortunately, it is not possible to collect material from the area around Mézières mentioned by Leidhold, as the Oxfordian is no longer exposed there (Dr. Maubeuge, personal communication 1965). As the specimen figured by Leidhold shows the internal structure, it seems probable that it was a silicified specimen from the "Terrain à Chailles".

The author has not been able to find the type specimens of either Oppel or Leidhold and it is considered highly unlikely that they still exist in a recognizable form. The neotype was collected from the "Terrain à Chailles" at Pagny-sur-Meuse, near Nancy, France.

DIMENSIONS OF NEOTYPE. Length 2.33 cm ; thickness 1.90 cm and width 2.60 cm.

MATERIAL. 25 specimens from Pagny-sur-Meuse (Meurthe et Moselle), including BB.44173, BB.44174.

DESCRIPTION. *External characters.* The outline of adult specimens is subpentagonal while that of the smaller ones is subtriangular ; the smaller specimens also tend to be equally biconvex while the larger ones have a more inflated brachial valve.

The beak is suberect and flanked by fairly well developed beak ridges. The interarea is relatively large and either flattened or slightly incurved. The deltidial plates are either disjunct or just conjunct. A large, well developed, circular pedicle opening is present and was presumably functional at all stages. Concentric ornament appears to be restricted to occasional, poorly developed growth lamellae.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.49 cm	1.73 cm	2.67 cm
2.33 cm	1.90 cm	2.60 cm

Internal characters. All the specimens available were silicified and much of the fine detail of the internal structure has been lost.

Pedicle valve. The narrow, elongated lateral cavities are delimited by slender, ventrally divergent dental lamellae which break away from the ventral wall of the valve well to the posterior of the plane of articulation. The teeth are strong and crenulated ; lateral denticulae are present.

Brachial valve. A septalium is present and can be clearly seen in text-fig. 32. It is less distinct in the other specimen sectioned, probably as a result of partial silicification. The crural bases are distinct and can be seen lying immediately behind the septalial plates in section 1, 5 of text-fig. 31 ; the crura are of the radulifer type. The hinge apparatus is strong with crenulated sockets and both inner and outer socket ridges well developed.

DISTRIBUTION. The distribution of the species is very uncertain and the only definite records are from the "Terrain à Chailles", of northern France and the Swiss Jura around Basel.

OCCURRENCE. The specimens collected by the author at Pagny were from sandy limestones containing cherty bands and nodules. The large associated fauna consisted of ammonites, lamellibranchs, mainly *Pholadomya* and *Lima* types, and *Thurmannella obtrita*. *T. obtrita* was the most abundant element and tended to

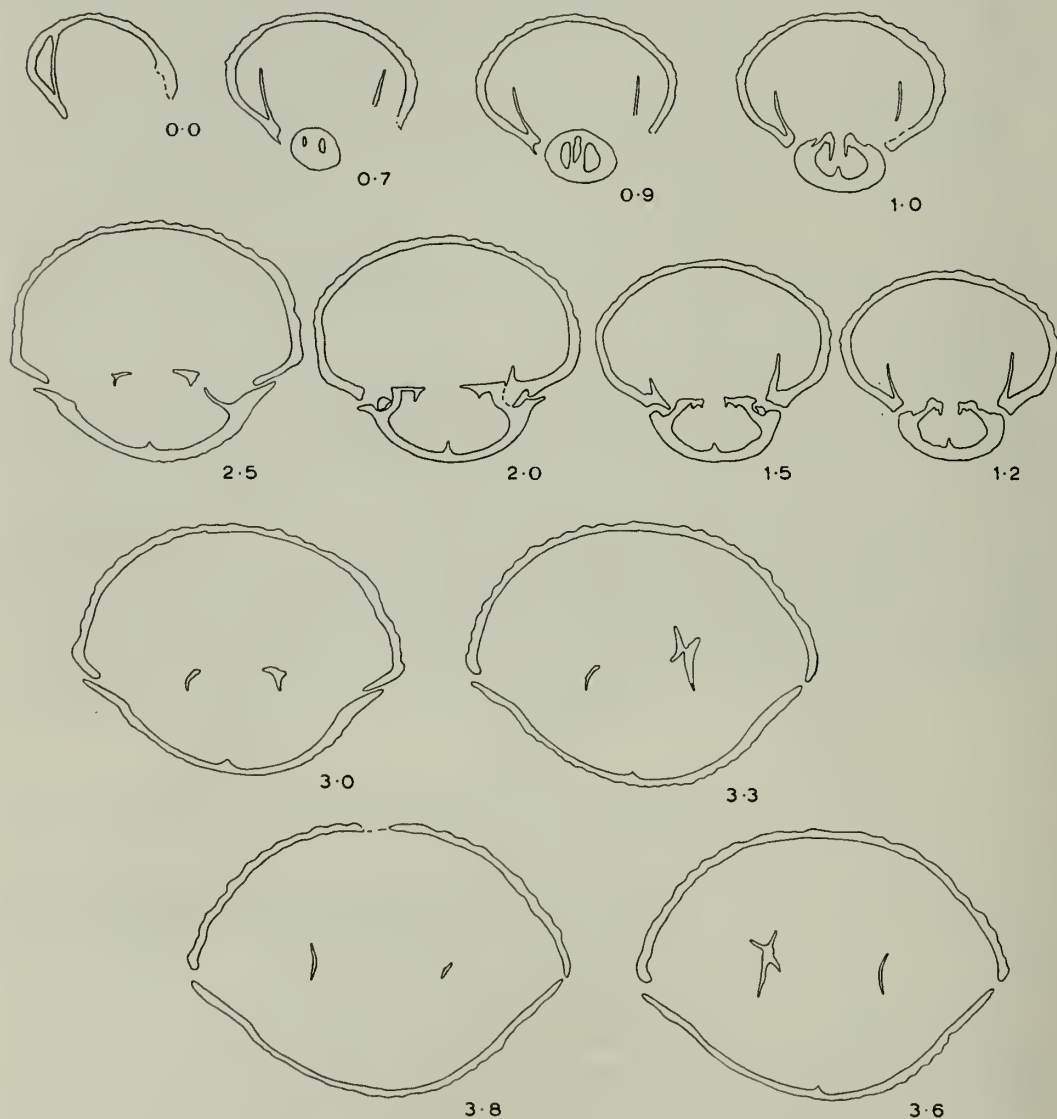


FIG. 31. Transverse serial sections of *Septaliophoria arduennensis* (Oppel). Oxfordian. "Terrain à Chailles". Pagny-sur-Meuse (Meurthe et Moselle). ($\times 3$).

occur in groups while *S. arduennensis* occurred as single specimens and was much less common.

REMARKS. The name *arduennensis* first appeared in the literature in 1858 when Oppel used it as a "n. sp." for, "*Rh. inconstans* d'Orb. 1848, Prodr. 13 460 (non Sow.)", in a list of Oxfordian fossils. He gave no description but subsequently included it in faunal lists from the ironstone of the Ardennes, as developed at Vieil-Saint Remy and Neuvizi, which he was describing together with other localities of his *Ammonites biarmatus* zone. However, he stated that he considered the above localities to be possibly of a higher horizon. Oppel's other citation of the species is from the "Zone des *Cidaris florigemma*. (Terr. à Chailles und unteres Coralrag)", of the Swiss Jura.

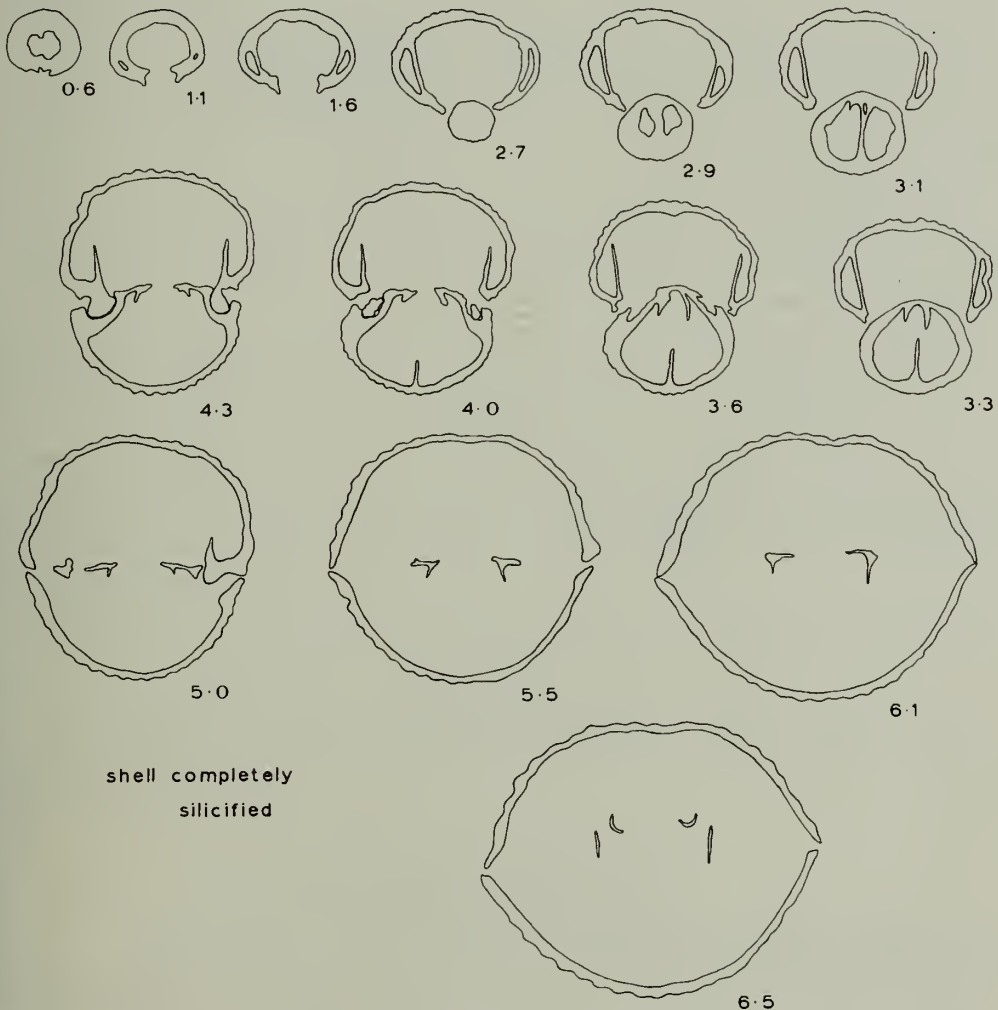


FIG. 32. Transverse serial sections of *Septaliphoria arduennensis* (Oppel). Oxfordian. "Terrain & Chailles". Pagny-sur-Meuse (Meurthe et Moselle), France. ($\times 3$).

Arkell (1956) thought the Neuvizy Ironstone to be of *cordatum* age, thus making it the lateral equivalent of the Terrain à Chailles which is *cordatum* and lower *transversarium* zones in age. This would then restrict *arduennensis*, as it was presumably conceived by Oppel, to those zones.

Oppel proposed a new name for Orbigny's *R. inconstans* as he realized that the Oxfordian species mentioned by Orbigny was not the one which had already been described by Sowerby (1821) under the name *inconstans* from the English Kimmeridgian. As Oppel was proposing *arduennensis* as a new name for *R. inconstans* of Orbigny, it seems reasonable to assume that the species to which he was referring exhibited some degree of asymmetry. Therefore, it seems fairly certain that by *arduennensis* he meant the medium sized asymmetrical rhynchonellid occurring quite frequently in the Lower Oxfordian of the areas mentioned by him. As can be seen from the figured specimens, the species shows varying degrees of asymmetry but is occasionally perfectly symmetrical. The latter condition is shown by the specimen figured by Leidhold and this again has led to some confusion. The species does not appear to have been figured other than by Leidhold and as *Terebratula inconstans* (pars) by Quenstedt.

In making *arduennensis* the type species of his new genus *septaliphoria*, Leidhold gave no description and merely commented that it came from the "Oxford-Stufe". The caption to the one specimen figured described it as coming from the "Oxford-Stufe" of Mézières.

Rollier (1917) suggested the possibility of *R. arduennensis* Oppel being a synonym of *Terebratulites helveticus* of Schlotheim (1813). The latter species was figured by Schlotheim but not given any description other than being listed as occurring in the "Jurakalkstein" near Basel and being given the citation "Scheuchzer (1718), fig. 105". The latter figure is virtually indeterminable except as a ribbed brachiopod. Although Rollier maintained that *R. helvetica* "est incontestablement une forme asymétrique de l'Oxfordian supér. et du Rauracien inférieur, très, fréquente dans le Jura aux environs de Bâsle," this statement seems to be erring on the side of optimism in view of inadequacy of the figures and the lack of detail given by both Scheuchzer and Schlotheim. Quenstedt (1871) considered the Schlotheim species to be his *Terebratula lacunosa multiplicata* from the "Malm gamma"; this does not appear likely but at least demonstrates the uncertain nature of the species. It therefore seems best to treat *T. helveticus* Schlotheim as a nomen dubium.

The *Terebratula helvetica* Schlotheim figured by Zieten (1831) possibly belongs to the genus *Septaliphoria*, but it is not considered to be conspecific with *S. arduennensis*.

Septaliphoria paucicosta sp. n.

(Pl. 9, figs. 5-6, text-fig. 33)

1878 *Rhynchonella lacunosa* (Schlotheim); Davidson: 196-97, pl. 16, figs. 13-14.

1917 *Rhynchonella helvetica* (Schlotheim); Rollier: 171.

NAME. Latin paucus-a-um, few; costa-ae, rib: the species has relatively few ribs.

DIAGNOSIS. Medium to large *Septaliphoria* ; 9-15 very coarse subangular ribs ; no smooth area posteriorly ; uniplicate or asymmetrical ; conjunct deltidial plates ; strong suberect beak ; crura radulifer.

STRATIGRAPHICAL RANGE. Oxfordian—*mariae* and *cordatum* zone ; the Lower Calcareous Grit of Yorkshire.

TYPE SPECIMEN. Holotype, BB. 45394, selected from a box of specimens in the collection of the B.M.(N.H.) with the locality given as " Hutton Bushell, Beedale, Yorkshire ".

DIMENSIONS OF HOLOTYPE. Length 2.61 cm, thickness 1.78 cm, width 2.90 cm.

MATERIAL. About 100 specimens, all from the collection of the B.M.(N.H.) B. 26924, B. 26903.

DESCRIPTION. *External characters.* The width is usually greater than the length, with the greatest width well towards the anterior giving the species a sub-pentagonal to subtriangular outline.

The beak is strongly developed in the smaller, more triangular specimens but is much less pronounced in the larger ones. Clearly marked beak ridges bound the strongly incurved interarea. An oval, submesothyridid pedicle opening is flanked by strongly conjunct deltidial plates.

The shell ornament consists solely of very coarse, steep, subangular ribs ; the size and coarseness of the ribbing readily distinguishes the species from *S. arduennensis*.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.58 cm	1.85 cm	2.90 cm
2.40 cm	1.87 cm	2.54 cm

Internal characters. Pedicle valve. The dental lamellae are subparallel and relatively short, breaking away from the valve wall well before the insertion of the teeth, as seen in transverse section. The teeth are strong and there are well developed lateral denticulae.

Brachial valve. A septalium is present and consists of strong septalial plates and a relatively weak median septum. The sockets show only weak crenulations ; inner and outer socket ridges are well developed.

The crura, which have clearly differentiated bases, are radulifer and curve towards the pedicle valve. At their distal ends they develop the curious processes which are also found in *S. arduennensis*.

DISTRIBUTION. As far as is known, the species has only been recorded from the type locality and from Filey Brigg (E. F. Owen, personal communication 1966).

REMARKS. The species only appears to have been mentioned twice in the literature. In 1878 Davidson tentatively referred the specimen he figured from Wykham to *Rhynchonella lacunosa* Schlotheim and in 1917, Rollier suggested that Davidson's specimen might be *R. helvetica* (Schloth.). As the species does not belong to the "lacunosa group" and *R. helvetica* is here regarded as a nomen dubium, a new species name has been proposed for these forms from the Lower Calcareous Grit.

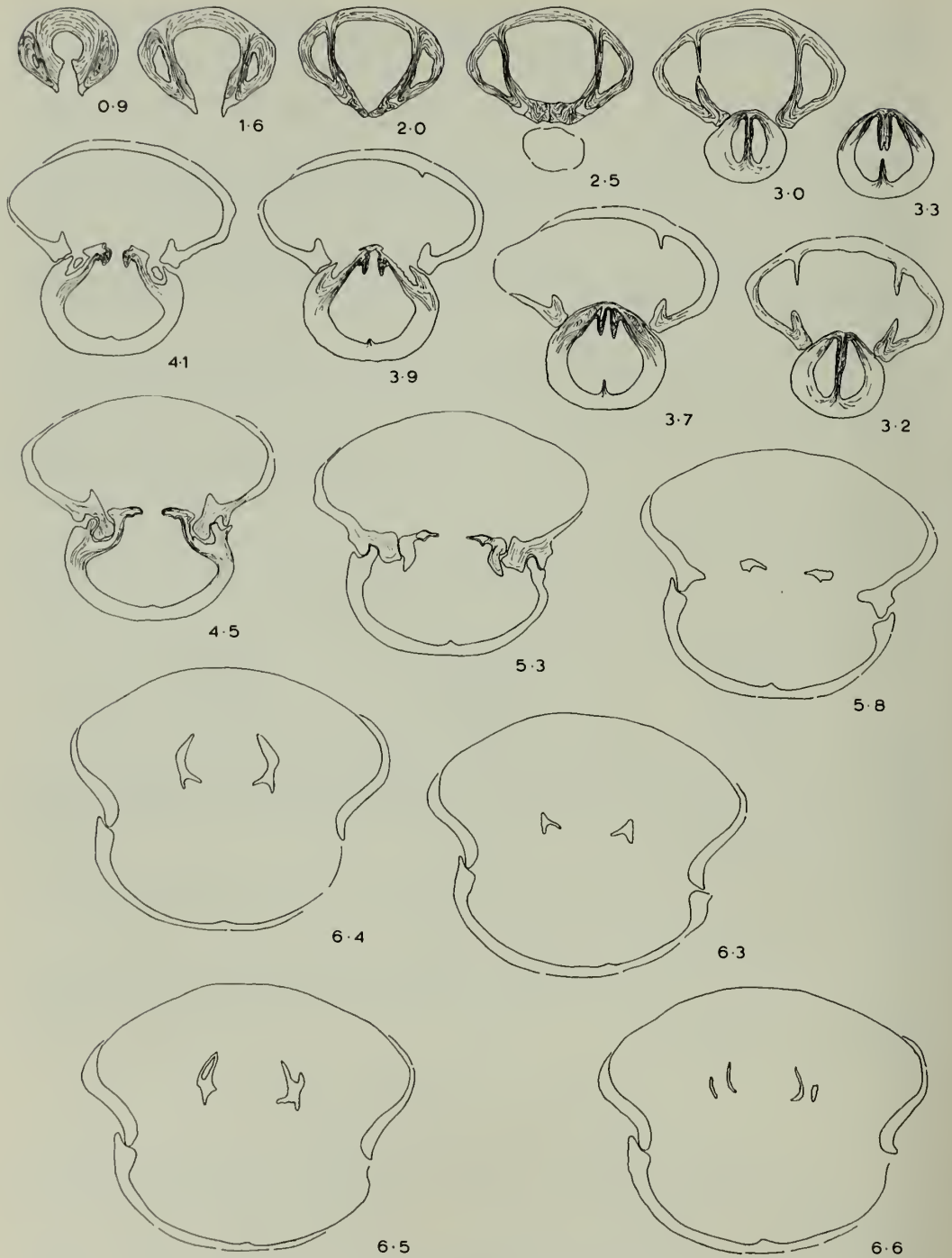


FIG. 33. Transverse serial sections of *Septaliphoria paucicosta* sp. nov. Topotype. Oxfordian. Lower Calcareous Grit. Hutton Bushell, Yorks. B.M. B 26924. ($\times 3$).

Septaliphoria (?) *hudlestoni* (Rollier)

(Pl. 9, figs. 1-4)

- 1878 *Rhynchonella pinguis* Roemer; Davidson: 193-94, pl. 16, fig. 7.
 1878 *Rhynchonella pinguis* var. *pectunculooides* Etallon; Davidson: 194-95, pl. 16, figs. 8-12.
 1917 *Rhynchonella Hudlestoni* Rollier: 172.
 1933 *Rhynchonella corallina* Leymerie; Arkell: 435.
 1947 *Rhynchonella pinguis* Roemer; Arkell: 87.

EMENDED DIAGNOSIS. Medium to large *Septaliphoria*-like form; 15-20 coarse, subangular ribs; uniplication in anterior commissure symmetrically or asymmetrically developed.

STRATIGRAPHICAL RANGE. Kimmeridgian—*cymodoce* zone.

TYPE SPECIMEN. Lectotype, here selected, fig. 10, plate 26 in Davidson (1878); collected from Abbotsbury Ironstone, Dorset. B.M. B. 27333.

MATERIAL. 34 specimens in the collection of the B.M.(N.H.) from Abbotsbury, Dorset, B. 26853-54, B. 26856, B. 26858, B. 26859. 8 specimens in author's collection, (from the same locality).

DESCRIPTION. *External characters.* In general the specimens are very poorly preserved. The species appears to be very variable; many of the specimens show asymmetrical development of the uniplication in the anterior commissure, although never the "bilobed" type of asymmetry found in *Torquirhynchia*. The globose specimens tend to show asymmetry more than the flatter ones which are often weakly trilobate in appearance; the latter forms also have a higher and more pronounced beak.

The beak ridges are very weak and the interarea is narrow and incurved. It would appear that the pedicle opening is small and circular but details of both this and the deltidial plates have not been satisfactorily observed. Radial ornament consists of about 15-20 coarse subangular ribs, while the only concentric ornament observed has been a few very weak growth lamellae on exceptionally well preserved specimens.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3.00 cm	2.60 cm	3.24 cm
2.73 cm	1.98 cm	2.78 cm
2.54 cm	1.70 cm	3.10 cm

Internal characters. An attempt was made to section an apparently well preserved specimen. Unfortunately, the external appearance was deceptive and virtually nothing could be seen of the internal structures except that a median septum and a possible septalium were present in the brachial valve. Mr. E. F. Owen (personal communication 1966) stated that he has attempted to section several specimens and in all cases it was impossible to determine the internal structure.

DISTRIBUTION. The only known occurrence of the species is in the Abbotsbury Ironstone of Dorset.

OCURRENCE. According to Arkell (1933), the brachiopods are restricted to the "ore bed" which he described as attaining a maximum thickness of 20 feet and as being a "crumbling reddish-brown oolitic rock, full of shining pellets of ore". The rhyntonellids are among the least abundant elements of a fauna which also includes the terebratulid *Ornithella lampas* (Sowerby), and various gasteropods, lamellibranchs and ammonites.

REMARKS. It has been decided to retain the specific name given by Rollier (1917) in preference to *Rhynchonella pinguis* Roemer and *R. pinguis* var. *pectunculoides* Etallon suggested by Davidson in view of the uncertainty attached to those names. If and when the latter species is revised, it may prove necessary to place the name *hudlestoni* in synonymy. This is considered unlikely, however, as the figures of *pectunculoides* given by Etallon (1861) appear to have finer ribs and a much stronger, more upright beak. *Rhynchonella corallina* Leymerie, the specific name suggested by Arkell, seems to be generally accepted as a synonym of *R. pinguis* Roemer, a species frequently quoted but greatly in need of elucidation and revision.

Septaliphoria (?) *septentrionalis* sp. n.

(Pl. 8, figs. 6-7)

NAME. Latin, septentrionalis—northerly; the species is only known to occur in the north of Scotland.

DIAGNOSIS. Flattened, medium sized *Septaliphoria*-like form; 10-15 strong, simple ribs; width greater than length.

STRATIGRAPHICAL RANGE. ? Upper Oxfordian—? Lower Kimmeridgian.

TYPE SPECIMEN. Holotype, BB. 44175, collected from Alt-na-cuile, near Brora, Sutherland.

DIMENSIONS OF HOLOTYPE. Length 2.37 cm, thickness 1.45 cm, width 2.86 cm.

MATERIAL. Further 20 specimens collected by the author from Alt-na-cuile; 6 specimens from collection of Royal School of Mines, presumably from the same locality. All the specimens are preserved as sandstone casts.

DESCRIPTION. *External characters.* The shell is either equally biconvex or with a slightly more inflated brachial valve. The beak is quite strong and suberect; details of the beak ridges and interarea are not preserved.

The only ornament preserved is the strong, simple ribs. Some specimens possess a posterior smooth area but it is not certain whether or not this is a result of the poor preservation. A slight uniplication was probably developed in some specimens, but in the best preserved material the anterior commissure tends to be asymmetrical.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.40 cm	1.73 cm	2.75 cm
2.35 cm	1.42 cm	2.85 cm

Internal characters. The preservation precludes serial sectioning and only very limited information can be obtained from the casts.

The dental lamellae are strong and divergent. The median septum also appears to be well developed and a possible septalium is indicated by one specimen.

DISTRIBUTION. The species is only known from the type locality.

OCCURRENCE. The species is found in the Alt na Cuile Sandstone which Arkell (1933) described as consisting of "thick beds of white sandstone separated by black carbonaceous layers". The associated fauna consists of lamellibranchs and ammonites; the rhynchonellids are the most abundant element of the fauna.

REMARKS. According to Arkell, the Alt na Cuile Sandstone has not yet yielded ammonites capable of defining precisely the zones present, although it is undoubtedly either topmost Oxfordian or basal Kimmeridgian. As the main fossil band is towards the top of the unit, it seems probable that the rhynchonellids are basal Kimmeridgian in age.

Arkell suggested that, as the rhynchonellids were the best preserved element of the fauna, it might be possible to use them to give a more accurate date to the strata. Unfortunately, there do not seem to be comparable forms of this age on the continent, probably as that area was largely occupied by coral and sponge reef facies, with their specialized faunas, while the Alt na Cuile Sandstone almost certainly represents a limited near-shore facies with a fauna presumably adapted to those conditions.

Although the poor preservation makes generic identification rather hazardous, the species is tentatively referred to *Septaliphoria* Leidhold. This determination is based on the relatively coarse, simple ribs and the fact that the anterior commissure may show either a symmetrical uniplication or be slightly asymmetrical; the internal characters visible are consistent with this designation; however, without more detailed information of the internal structures, which is unlikely to be forthcoming, it is not considered that a definite generic diagnosis is possible. Davidson (1878) suggested that the casts from Alt-na-cuile, "may also probably be referable to Schlotheim's species (*Rhynchonella lacunosa*)". It can be safely stated that *S. (?) septentrionallis* does not belong to the genus *Lacunosella*.

Genus **TORQUIRHYNCHIA** nov.

1886 *Inconstans*-Sippe (pars) Rothpletz, p. 91.

1918 *Rhactorhynchia* (pars) Buckman, pp. 50-52.

1932 *Septaliphoria* (pars) Wiśniewska, pp. 18-20.

NAME. Latin se torquere—to twist: all members of the genus are markedly asymmetrical.

TYPE SPECIES. *Terebratula inconstans* Sowerby.

DIAGNOSIS. Large, asymmetrical rhynchonellids with coarse, simple ribbing; septalial plates reduced or absent; median septum present but usually very weakly developed; crura radulifer.

STRATIGRAPHICAL RANGE. In Europe the species appears to be restricted to the Kimmeridgian and lower Volgian; however, Makridin (1964) has figured specimens from the Russian Platform which appear to belong to *Torquirhynchia* and which include material from the upper Oxfordian and the middle and upper Volgian.

DESCRIPTION. *External characters.* The most characteristic feature is the strong asymmetry exhibited by all the species, as viewed from the anterior. The "twist" occurs indiscriminately either to the right or to the left. A fold and uniplication are never developed. Each valve has 20-30 angular or subangular ribs which are almost invariably simple, arising from the umbones; however, bifurcation has occasionally been observed postero-laterally in *T. guebhardi* and *T. speciosa*.

The strong beak is usually suberect although in specimens with a very inflated brachial valve, notably in *T. inconstans*, it may be adpressed to that valve. Except in the latter case, a functional pedicle opening is present and is flanked by disjunct to strongly conjunct deltidial plates.

Internal characters. Pedicle valve. The lateral cavities and dental lamellae are rather variably developed, ranging between massive lamellae and correspondingly small lateral cavities and larger cavities bounded by slender lamellae. A slight pedicle collar may be developed. Strong, crenulated teeth and well developed lateral denticulae characterize the hinge apparatus.

Brachial valve. A low, relatively long median septum is present; septalial plates occur in all the species investigated, although they are of a distinctively reduced form. Inner and outer socket ridges are both well developed; the socket floors are strongly crenulated.

The crural bases differ quite markedly in their development in the different species described. Although the crura are radulifer in general appearance, they show considerable variation towards their distal ends. It is not known whether the development of these various distal processes can be regarded as consistent at species level.

SPECIES. The following nominal species are attributed to the genus:

- T. "astieriana"* (Orbigny) (in Haas, 1891, p. 62, pl. viii, figs. 3-6, pl. ix, figs. 1-9)
- T. "astieriana"* (Orbigny) (in Makridin, 1964, pp. 107-9, pl. ii, fig. 8)
- T. "astieriana"* (Orbigny) (in Wiśniewska, 1932, p. 20, pl. i, figs. 21-26)
- T. astieriformis* (Wiśniewska) (1932, pp. 27-28, pl. i, figs. 19 ?20)
- T. inconstans* (Sowerby) (1821, vol. III, p. 137, pl. 277, fig. 4)
- T. guebhardi* (Jacob & Fallot) (1913, p. 44, pl. v, fig. 9)
- T. pseudo-inconstans* (Kitchin) (1900, pp. 51-2, pl. x, figs. 6-10)
- T. lehmanni* (Makridin) (1964, pp. 109-10, pl. ii, fig. 9)
- T. pectunculoides* (Etallon) (1861, p. 289, pl. xlii, fig. 3)
- T. semiconstans* (Etallon) (1861, p. 290, pl. xlii, fig. 4)
- T. speciosa* (Münster) (1839, p. 113, pl. xiii, fig. 6).

DISTRIBUTION. Although individual species appear to be relatively restricted geographically, the genus, taken as a whole, occurred over much of Europe west of the Alps. If the species of Makridin mentioned above have been correctly assigned, then the genus was also present on the Russian Platform.

OCCURRENCE. The genus appears, from the limited information available, to have been restricted to peri-reefal areas, and it is suggested that the asymmetrical development may represent an adaptation for living in a high energy environment.

REMARKS. The genus *Torquirhynchia* has been proposed in order to group together the various distinctively asymmetrical rhynchonellid species of the Upper Jurassic. Many of the included species have previously been attributed to *Rhynchonella astieriana* Orbigny.

The Upper Jurassic, asymmetrical rhynchonellids have also been frequently referred to the genus *Septaliphoria* Leidhold, largely as a result of the paucity of generic names at this stratigraphical level and the lack of information regarding the diagnostic characters of the type species of that genus, namely *S. arduennensis* (Oppel). Internally, *Torquirhynchia* is readily distinguished from *Septaliphoria* by its weakly developed septalial plates and the position and development of the crural bases relative to them. Externally, the adult specimens of *Torquirhynchia* attain a much greater size and are always strongly asymmetrical whereas specimens of *Septaliphoria* are only weakly asymmetrical or are symmetrical.

***Torquirhynchia inconstans* (J. Sowerby)**
(Pl. 10, figs. 1-3, pl. 12, fig. 5, text-fig. 34)

- 1821 *Terebratula inconstans* J. Sowerby: 137, pl. 278, fig. 4.
 1834 *Terebratula inconstans* J. Sowerby; Buch: 45-46.
 1838 *Terebratula inconstans* J. Sowerby; Buch: 146, pl. 14, fig. 16.
 1852 *Rhynchonella inconstans* (J. Sowerby); Davidson: 87-88, pl. 18, figs. 1-3.
 1878 *Rhynchonella inconstans* (J. Sowerby); Davidson: 191-93, pl. 16, figs. 1-6.
 1917 *Rhynchonella inconstans* (J. de C. Sowerby) (sic); Rollier: 177-78.
 1918 *Rhactorhynchia inconstans* (J. Sowerby); Buckman: 51.

EMENDED DIAGNOSIS. Medium sized, globose *Torquirhynchia*; strongly developed beak ridges and interarea; 25-30 simple angular ribs; crura radulifer.

STRATIGRAPHICAL RANGE. Kimmeridgian—*baylei* to *cymodoce* zones.

TYPE SPECIMEN. Lectotype, here selected, fig. 4, pl. 277 of Sowerby (1821); the specimen is from the Kimmeridge Clay of Ringstead Bay, Dorset, in B.M.(N.H.) Sowerby Coll. No. B. 61475.

MATERIAL. More than 100 specimens from the collection of the B.M.(N.H.) mostly from the Dorset Coast but also including a limited number of specimens from inland localities. 10 specimens in the author's collection obtained from Ringstead Bay.

DESCRIPTION. *External characters.* The shell outline is subpentagonal and the valves are equally biconvex. The radial ornament consists of about 25-30 simple, angular or subangular ribs which show neither intercalation nor bifurcation, while the concentric ornament consists of numerous fine growth lines and occasional weak growth lamellae. In the flatter specimens the strongly developed beak is erect but the extent of the incurvature is obviously dependent on the globosity of the shell and in very globose specimens the beak is adpressed to the brachial valve.

The relatively small hypothryridid or submesothyridid pedicle opening is flanked by small disjunct or conjunct deltidial plates. Beak ridges are clearly marked and bound the well developed interarea; the latter may be flattened but is usually strongly incurved.

The asymmetrical development usually commences when the animal is about half grown and becomes increasingly pronounced with age.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3·20 cm	3·10 cm	3·25 cm
3·02 cm	2·64 cm	3·12 cm
3·20 cm	2·25 cm	3·31 cm

Internal characters. Pedicle valve. The shell wall is very thick and the small lateral cavities are not seen in transverse section until about the level of the top of the brachial valve. The dental lamellae are massive and only attached to the ventral shell wall at their extreme posterior ends. The teeth are strong and heavily crenulated; the general impression given by the teeth, dental lamellae and the way the pedicle valve abuts against the brachial valve in the earlier sections, is that the species possessed a very strongly articulated shell.

Brachial valve. The sockets are crenulated and there are both inner and outer socket ridges. A median septum is present but it does not come into contact with the septal plates as it is only present posteriorly as a low ridge. The septum completely disappears, as seen in transverse section, before the end of the crura is reached, but shows quite a strong development for part of its length. The distinctive short, rounded septal plates are seen on the dorsal side of the ventrally curved hinge plates. Crural bases are hardly differentiated. At first, as seen in transverse section, the radulifer crura appear as structures flattened in the plane of articulation, but in later sections they become more rod-like and finally become flattened at right angles to the plane of articulation and curve towards the pedicle valve.

DISTRIBUTION. The best known localities are those of Ringstead Bay and Weymouth in Dorset; inland, it has been recorded from Shotover Hill near Oxford, Wooton Bassett in Wiltshire, Brill in Buckinghamshire and from Swindon. On the continent as observed by Haas (1890), the species appears to be restricted to north-western France. Buch (1838) recorded it from Ellrichserbring in Brunswick. His figure of the species is a copy of Sowerby's (1821) figure 4 and, as he did not illustrate any material from his locality, the record must be regarded as doubtful.

OCCURRENCE. At Ringstead Bay it occurs in a thin bed of pale grey clay, lying between the Ringstead Coral Bed and the Exogyra Bed, as illustrated in Arkell (1933, pl. 21). The associated fauna includes terebratulids, the gasteropod *Bathrotomaria reticulata* (Sowerby) and ammonites. Ager (1965a) has drawn attention to the probability of *T. inconstans* living in a peri-reefal environment, as evidenced by the close proximity of the Coral Bed. At Shotover Hill it is recorded by Phillips (1855) as occurring in a band of septarian nodules in a shaly clay of *cymodoce* age.

REMARKS. In his discussion of the species, Davidson (1852) included a specimen (pl. 18, fig. 4) from the Inferior Oolite of Leckhampton Hill. The author has not seen the actual specimen, but assumes this to be a misidentification in view of the otherwise restricted record of the species. On the same plate fig. 3, Davidson figured a symmetrical specimen from Shotover Hill, again the author has not seen the

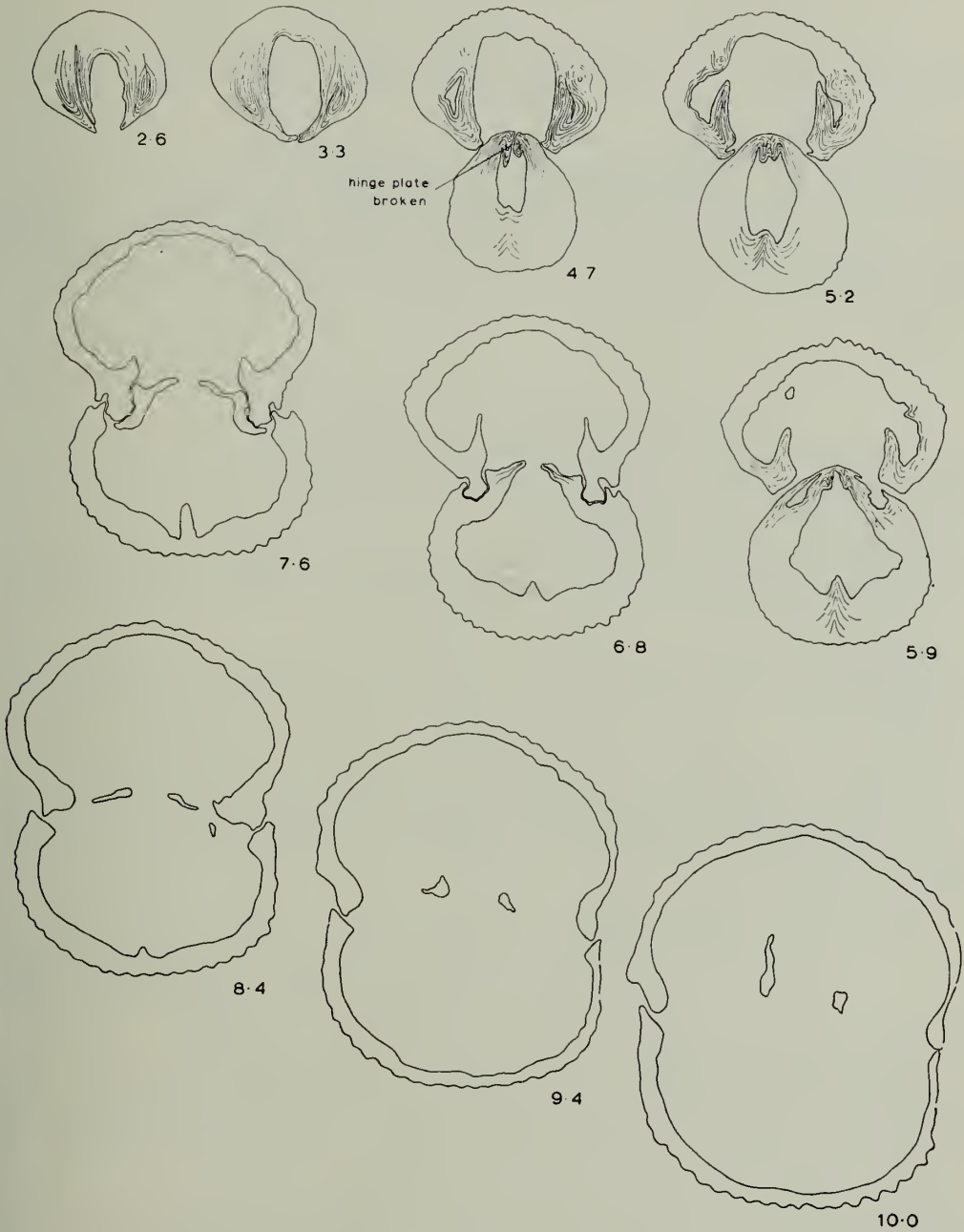


FIG. 34. Transverse serial sections of *Torquirhynchia inconstans* (Sowerby). Topotype. Kimmeridgian. Kimmeridge Clay. Ringstead Bay, Dorset. ($\times 2$).

specimen but it seems unlikely that it is correctly determined as, apart from its symmetry, the ribbing and general shape also differ from *inconstans*. The B.M. (N.H.) collection contains only one symmetrical specimen attributed to *inconstans*, a large trilobate form again from Shotover Hill. The horizon of this specimen is not known but, despite crushing, it is interesting in that it appears closer to *Somalirhynchia sutherlandi* than to *T. inconstans*.

While collecting material at Ringstead Bay, it was obvious that a fairly high proportion of the specimens obtained were unusual in that the valves "gaped". The author has since examined the specimens available at the B.M.(N.H.), about 100, and this has confirmed that about a third show this feature. Many specimens have a well developed epifauna and the tubes of ?*Serpula* are frequently seen on both valves.

Torquirhynchia guebhardi (Jacob & Fallot)
(Pl. 10, figs. 4-6, text-fig. 35)

1913 *Rhynchonella Astieriana* Orbigny var. *Guebhardi* Jacob & Fallot: 45-46, pl. 5, fig. 9.

1917 *Rhynchonella Guebhardi* Rollier: 77.

EMENDED DIAGNOSIS. Medium-sized, globose *Torquirhynchia*; markedly asymmetrical with a frontal notch between the two lobes; about 30 subangular ribs; radulifer crura flattened in the plane of articulation.

STRATIGRAPHICAL RANGE. Jacob & Fallot describe it as coming from the "Portlandien"; the author has collected it from the *cymodoce* zone of the Kimmeridgian.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Jacob & Fallot (1913), pl. 5, fig. 9; the type locality is St. Vallier (Alpes-Maritimes).

MATERIAL. 7 specimens from a road cutting north of Lac d'Armaille (Ain) in British Museum (Nat. Hist.) nos. BB. 45762-68. Other localities in the southern Jura from which the species has been collected include Rossillon, Glandieu, Brognin Hill and Chavoley.

DESCRIPTION. *External characters.* The valves are almost equally biconvex, with a tendency for the brachial to be slightly the more inflated. However, the valves are distinctively very globose and this, coupled with the very strongly developed asymmetry, differentiates *T. guebhardi* from other species in the genus. The beak is sharp and suberect and the shell outline subtriangular.

T. guebhardi possesses about 30 relatively fine, subangular ribs which arise at the umbones and continue simply to the anterior margin; bifurcation has only been observed in a few postero-laterally positioned ribs. The concentric ornament consists only of rather sparse, weak growth lamellae.

Although the beak is quite large and suberect, the beak ridges are only weakly developed as are the small, incurved interareas. An oval, submesothyridid pedicle opening is flanked by conjunct deltidial plates. In transverse section the deltidial plates are clearly seen to project externally around the foramen.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.97 cm	2.20 cm	3.35 cm
2.55 cm	1.95 cm	2.80 cm

Internal characters. Most of the fine detail of the structures has been lost through recrystallisation.

Pedicle valve. The narrow, elongate lateral cavities, which penetrate almost to the apex of the beak, are limited by slender dental lamellae. A pedicle collar is present. The teeth are strong and crenulated; lateral denticulae are present but not strongly developed.

Brachial valve. There is no septalium and only a weak median septum; small septalial plates are present. The sockets are crenulated; inner and outer socket ridges well developed. Crural bases are not well differentiated. The radulifer crura are flattened in the plane of articulation and do not curve towards the pedicle valve.

DISTRIBUTION. The species only appears to have been recorded from the following two areas. (1) The material of Jacob & Fallot (1913) came from St. Vallier in the French Alpes Maritimes and in the "Portlandien coralligène des environs de Gerin, Ain". The latter name is probably a mis-spelling of Cerin. (2) All the material studied by the author was collected by various members of Imperial College from the southern French Jura in the area around Belley, which is also in the Département of Ain.

OCCURRENCE. The material described by the author was collected from the Bedded Virieu Limestone (Ager and Evamy, 1963). The following description of mode of occurrence and lithology is taken from Evamy (1963), "The subdivision (of the Bedded Virieu containing *T. guebhardi*) is about 20 m thick—it consists mainly of alternating limestones and shales, which yield an abundant brachiopod, lamellibranch fauna, as well as ammonites of the *tenuilobatum* and *pseudomutabilis* zones—. The limestones are thinly bedded (20–40 cm) brown calcilitites, occasionally showing a mottled iron-staining. These are separated by thin (approximately 10 cm) shaly bands." He also noted that, "A few thicker beds of calcilitite (1–1½ m) are seen not to contain the abundant mollusc and brachiopod fauna." The beds containing *T. guebhardi* immediately underlie the reef horizon of the Massive Virieu Limestone.

REMARKS. Although the author has not seen the original material of *Rhynchonella Astieriana* var. *Guebhardi*, it is thought that a conspecific identification for the material from the Bedded Virieu Limestone can confidently be given as it matches exactly the specimen figured by Jacob & Fallot (1913). Also, the Bedded Virieu could well be the lateral stratigraphical equivalent of the "Portlandien" of Jacob and Fallot. Referring to the Bedded Virieu, Ager and Evamy (1963) note that it is, "strongly reminiscent of the 'Tithonien' facies seen in many parts of Europe at this level". In the latter publication, *T. guebhardi* is referred to as *Septaliphoria astieriana* (d'Orbigny).

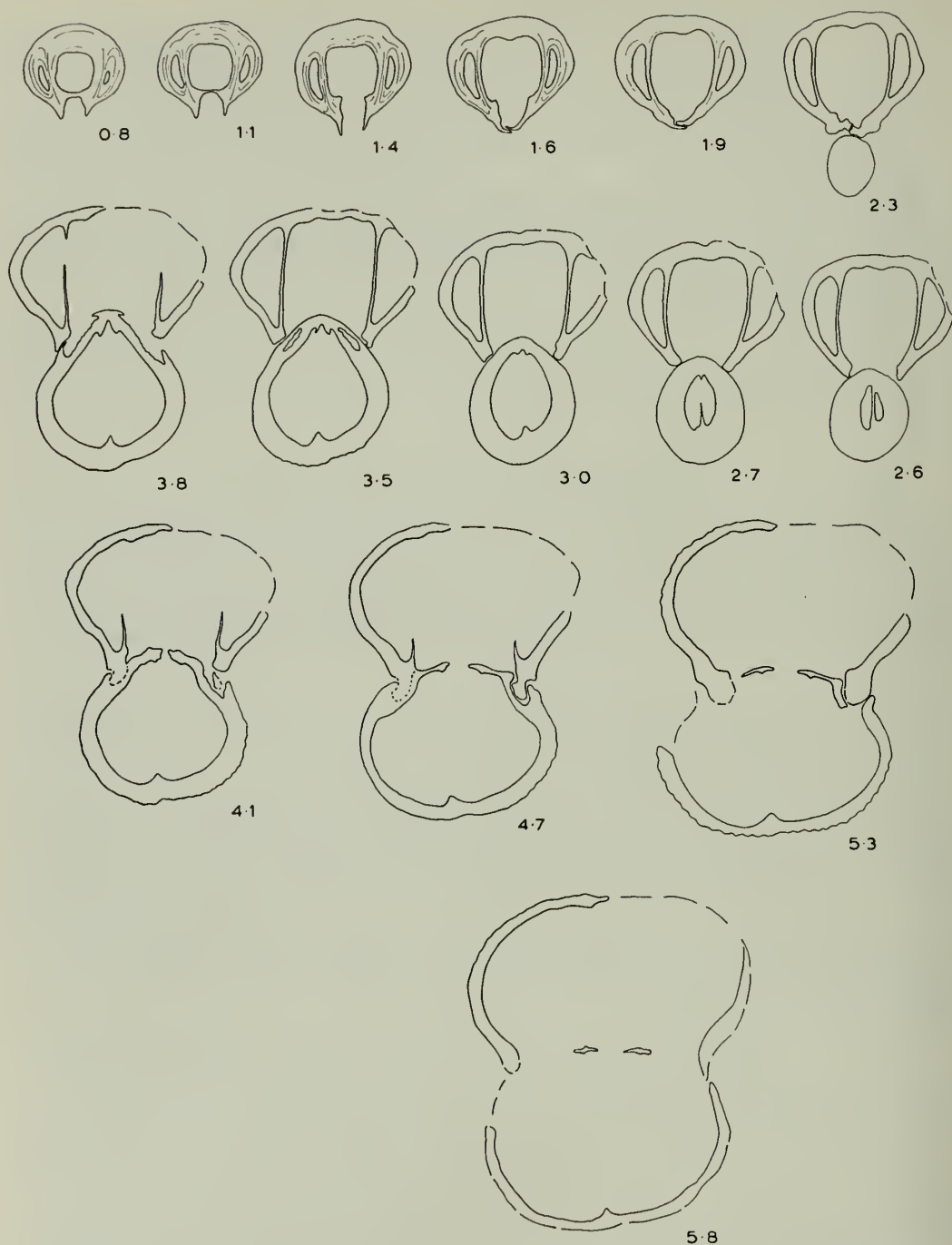


FIG. 35. Transverse serial sections of *Torquirhynchia guebhardi* (Jacob & Fallot). Kimmeridgian—*cymodoce* zone. N. of Lac d'Armaile (Ain), France. ($\times 3$).

Torquirhynchia cf. *T. astierformis* (Wiśniewska)

(Pl. 12, figs. 1-3, text-fig. 36)

1932 *Septaliphoria pinguis* (Roemer) var. *astierformis* Wiśniewska: 27-28, pl. 1, fig. 19, ?20.

EMENDED DIAGNOSIS. Relatively flattened, medium sized *Torquirhynchia*; about 20 subangular ribs; beak small; asymmetrical development not sufficient to produce a frontal notch; crura radulifer.

STRATIGRAPHICAL RANGE. The material described by the author came from the *mutabilis* zone of the Kimmeridgian, while the specimens figured by Wiśniewska came from the "Rauracien sup." and "Kimmeridgien?"

MATERIAL. 6 specimens collected by the author from Sermérieu (Isère), including B.M. BB.45174, BB.45175, BB.45176.

DESCRIPTION. *External characters.* The width is greater than the length and the greatest width is towards the anterior; this, combined with the rather steep apical angle, results in an overall subtriangular outline. *T. cf. T. astierformis* is equally biconvex and relatively flattened as compared with other species of the genus. The coarse ribs arise at the umbones and continue simply to the anterior margin; concentric ornament has not been observed.

The beak is suberect and flanked by slight beak ridges which delimit the weakly developed and slightly incurved interarea. Disjunct deltidial plates define the relatively small pedicle opening. Asymmetry is characteristic but is not so marked as in *T. guebhardi* as it does not result in the development of a frontal notch.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3.18 cm	2.55 cm	3.49 cm
2.63 cm	2.94 cm	3.00 cm
2.32 cm	2.47 cm	2.73 cm

Internal characters. Pedicle valve. The lateral cavities are bounded by strong, subparallel dental lamellae which break away from the ventral wall of the valve, as seen in transverse section, before the insertion of the teeth. The teeth are strong and crenulated; well developed lateral denticulae are present.

Brachial valve. The sockets show tegulate crenulations and both inner and outer socket ridges are strongly developed. The redulifer crura curve towards the pedicle valve; at their distal ends they produce the rather peculiar processes seen in text-fig. 36.

DISTRIBUTION. As stated above, the author's material came from Isère where, according to Dr. Enay (personal communication 1964), it is not an uncommon species. The only figured material likely to be conspecific is that of Wiśniewska (1932) from Poland.

OCCURRENCE. The species was collected from irregularly interbedded, fine grained limestones and marls. The exposure consisted of a small roadside cutting and the varied fauna present was largely collected from around a small sponge reef about 1 m high and 2 m across. Apart from the rhynchonellids, the fauna included

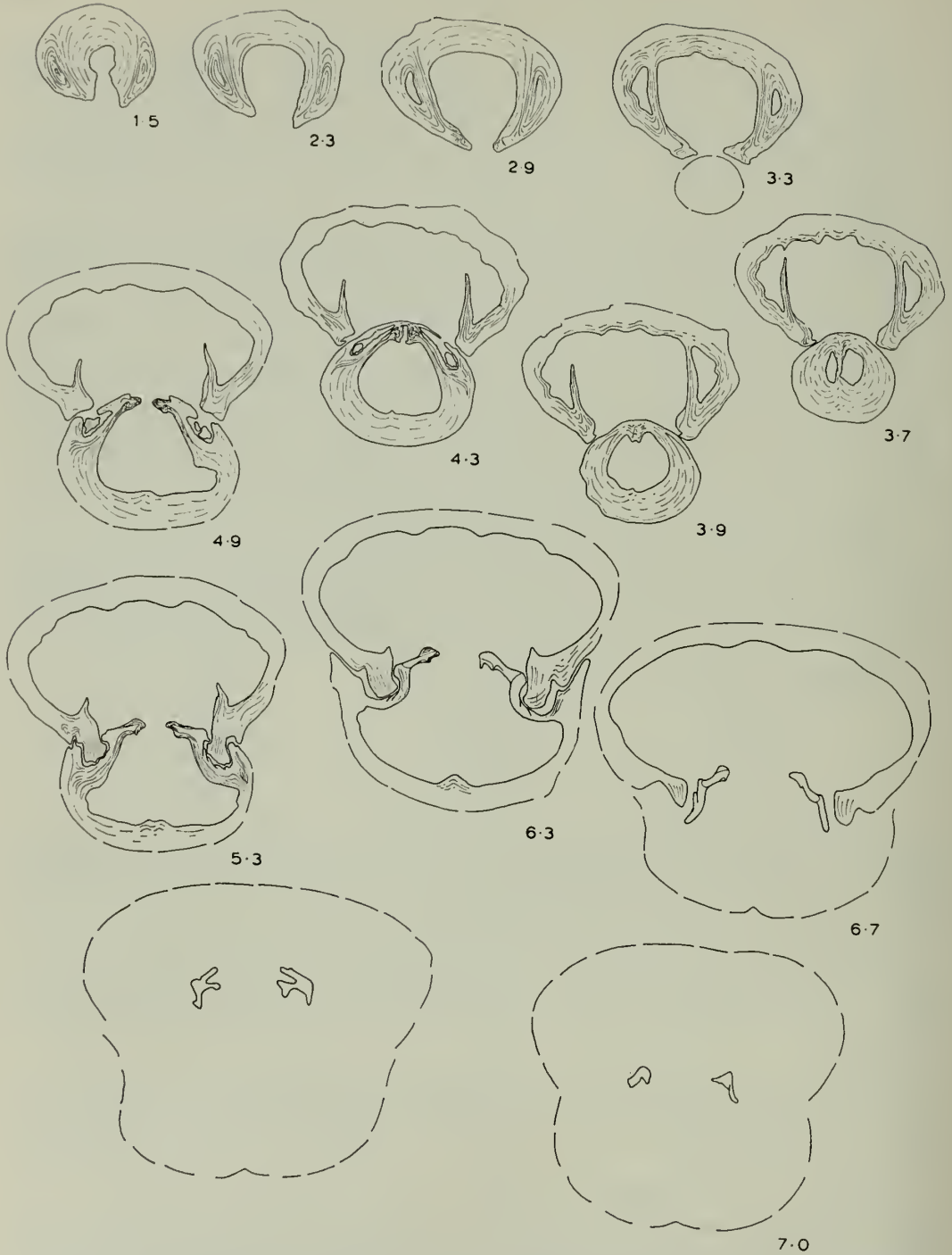


FIG. 36. Transverse serial sections of *Torquirhynchia* cf. — *astieriformis* (Wiśniewska).
Kimmeridgian—*mutabilis* zone. Sermérieu (Isère), France. ($\times 3$).

crinoid ossicles, zeilleriids and terebratulids as well as sponges. The rhynchonellids were interesting in that the two species present belonged to two different genera namely, *Torquirhynchia* and *Lacunosella*; both species were associated with the sponges and Dr. Enay stated that this is a characteristic association of the *mutabilis* zone in that area. *T. cf. astieriformis* was the least abundant element of the fauna.

REMARKS. Although externally one, at least, of the specimens figured by Wiśniewska very closely resembles the material from Isère, the lack of records from the intervening area and the lack of knowledge as to the internal structures of the Polish material precludes a definite conspecific identification of the French and Polish specimens.

Torquirhynchia speciosa (Münster)

(Pl. 11, figs. 1-3, text-fig. 37)

- 1832 *Terebratula difformis* Lamarck; Zieten: 56, pl. 62, figs. 2.
 1839 *Terebratula inconstans speciosa* Münster: 113, pl. 13, fig. 6.
 1847 *Rhynchonella Astieriana* Orbigny: 14-15, pl. 492, figs. 1-4.
 1850 *Rhynchonella Astieriana* Orbigny; Orbigny: 24.
 1852 *Terebratula inconstans* Quenstedt: 455, pl. 36, fig. 44.
 1858 *Rhynchonella Astieriana* Orbigny; Suess: 52, pl. 6, fig. 2.
 1863 *Rhynchonella inconstans* Orbigny; Ooster: 47, pl. 15, figs. 1-13.
 1871 *Terebratula inconstans speciosa* Quenstedt: 138-39, pl. 15, figs. 45, 51, ?50.
 1885 *Terebratula inconstans* Quenstedt: 694, pl. 53, fig. 64.
 1913 *Rhynchonella Astieriana* Orbigny; Jacob & Fallot: 43, pl. 5.
 1917 *Rhynchonella Astieriana* Orbigny; Rollier: 176.
 1917 *Rhynchonella speciosa* Rollier: 178.

EMENDED DIAGNOSIS. Largest known species of *Torquirhynchia*, being up to 10 cm wide; 20-30 coarse, angular ribs; large prominent suberect beak; asymmetrical; width always greater than length; crural bases sharply pointed; crura radulifer.

STRATIGRAPHICAL RANGE. Kimmeridgian—lower Volgian: limestones in which topotypes occur range from *subeumela* to *Gravesia* zones (Dr. Barthel, personal communication 1965).

TYPE SPECIMEN. Lectotype, here selected, is the specimen originally figured by Münster, pl. 13, fig. 6; a plaster cast of this is in the collection of the B.M.(N.H.), B. 5513.

DIMENSIONS OF LECTOTYPE. Taken from plaster cast mentioned above: length 5.22 cm, thickness 3.35 cm, width 7.92 cm.

MATERIAL. 28 specimens in the collection of the author including B.M. BB.45171, BB.45173 from Saal, Germany. 2 specimens from collection of the University of Tübingen.

DESCRIPTION. *External characters.* *T. speciosa* is one of the largest Mesozoic rhynchonellids: Quenstedt (1871) recorded a specimen over 10.0 cm wide. The species shows considerable variation in outline but, as the greatest width is well toward the anterior, it is usually subtriangular or suboval. There are about 20-30

very strong, sharply angular ribs which arise from the umbones and continue simply to the anterior margin. Concentric ornament, not always preserved, consists of numerous fine growth lines, together with occasional coarser growth lamellae.

The species has a characteristically strong, high, suberect beak which is flanked by a large, well-marked interarea, although the beak ridges limiting these are only weakly developed. *T. speciosa* possesses a large hypothrydid pedicle opening.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
5.50 cm	2.30 cm	6.87 cm
4.73 cm	2.42 cm	5.00 cm
2.60 cm	1.70 cm	3.05 cm

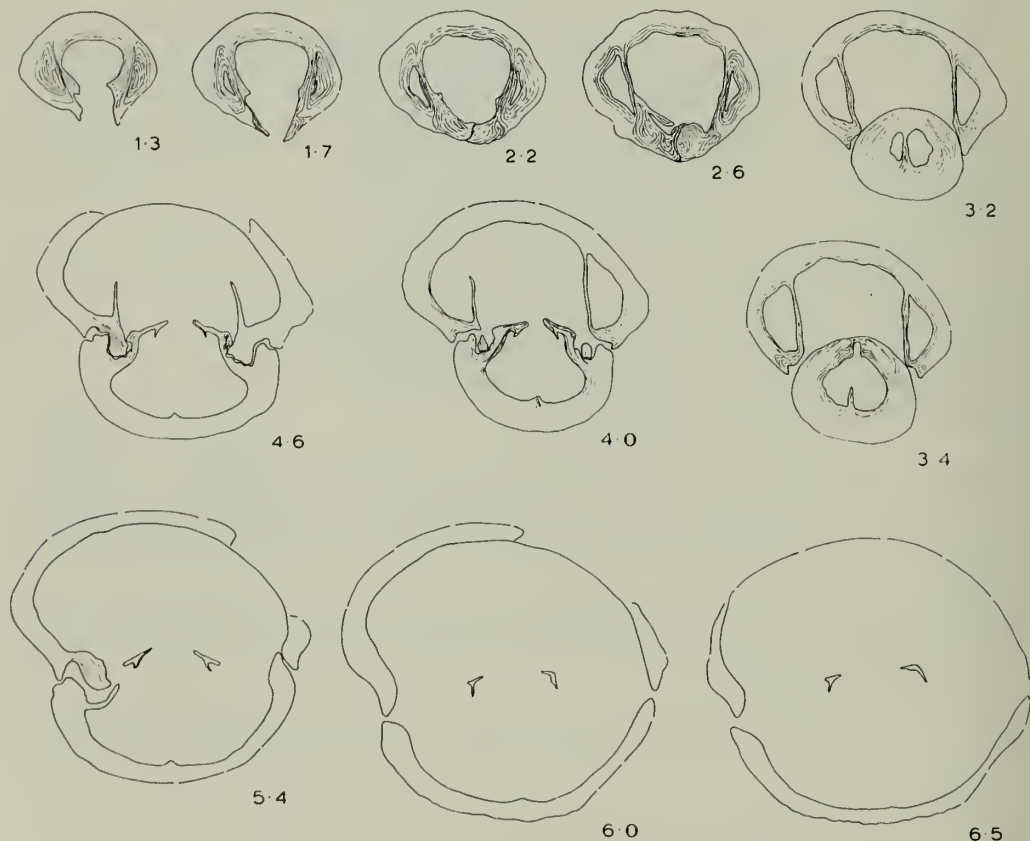


FIG. 37. Transverse serial sections of *Torquirhynchia speciosa* (Munster). Kimmeridgian/Lower Volgian. "Diceras Kalk". Saal, Germany. ($\times 3$).

Internal characters. Pedicle valve. There is a weakly developed pedicle collar. The deltidial plates project slightly, "reinforcing" the pedicle opening; below the level of the pedicle opening they become conjunct and then "crumple up" against one another. Relatively slender, subparallel dental lamellae are present. The teeth are strong and crenulated; there are well developed lateral denticulae.

Brachial valve. The median septum is weak and there are no septalial plates. The crural bases are clearly differentiated. The radulifer crura are relatively small and curve only slightly to the ventral of the plane of articulation. The sockets show tegulate crenulations ; inner and outer socket ridges are both strongly developed.

DISTRIBUTION. Judging from the figures and descriptions in the literature, the species has a rather discontinuous distribution. The material figured by Zieten (1832), Münster (1839) and Quenstedt (1852, 1871, 1885) came from the Franconian and Swabian Jura, while the type localities for *Rhynchonella Astieriana* of Orbigny (1847) are in the French "Alpes Maritimes" at Escragnoles and La Malle. Other figured specimens which would appear to be conspecific are from "Les Alpes Bernoises et Vaudoises" (Ooster, 1863), and from Stramberk, Czechoslovakia, and adjacent areas of Poland (Suess, 1858).

OCCURRENCE. At Saal, *T. speciosa* is associated with a very varied fauna which includes many large species, or at least large specimens, of terebratulids, gasteropods and lamellibranchs. One of the most distinctive elements here is the lamellibranch *Diceras*, which gives its name to the limestone. Dr. Barthel (personal communication 1965) suggests that the Diceras-Kalk, as seen at Saal and Kelheim, represents a fore-reef limestone. Unfortunately, the details at Saal are largely obscured by the recrystallization, tectonics and fissure infillings of younger material.

REMARKS. Although the name *Rhynchonella Astieriana* of Orbigny (1847) has been very widely used and is embedded in the literature, it is an indisputable objective junior synonym of *Terebratula inconstans speciosa* of Münster (1839). In his original description of *R. Astieriana* Orbigny gave Münster's species in his synonymy and as, under the present rules of nomenclature, it is not permitted to arbitrarily replace a specific or subspecific name with another, Münster's name *speciosa* must be given priority. Since Orbigny, it appears that only Quenstedt (1871) has described *Astieriana* as a synonym of *speciosa* while other authors such as Suess (1858) and Haas (1870) have either retained the name *Astieriana* while admitting *speciosa* as a synonym of it, or ignored *speciosa* altogether, e.g., Jacob and Fallot (1913). In general, the name *Astieriana* has tended to be used for all rhynchonellids in the Upper Jurassic showing asymmetry.

Terebratula difformis of Zieten is a junior homonym of *T. difformis* of Lamarck.

"*Rhynchonella*" *ordinaria* sp. n.

(Pl. 9, figs. 7-11, text-figs. 38-39)

NAME. Latin *ordinarius*-a-um, ordinary ; the species is a very "ordinary looking" rhynchonellid.

DIAGNOSIS. Medium sized rhynchonellid ; strong suberect beak ; 15-20 simple, subangular ribs ; there is a weak median septum ; septalial plates present but only poorly developed ; crura radulifer.

STRATIGRAPHICAL RANGE. Of the two occurrences of the species known one is in the *pseudocordata* zone of the Oxfordian and the other is in the "Sequanien".

TYPE SPECIMEN. Holotype, BB. 45167, was obtained from the *pseudocordata* zone at Mont Dolet near Sermérieu (Isère), France.

DIMENSIONS OF HOLOTYPE. Length 2.50 cm, thickness 1.78 cm, width 2.20 cm.

MATERIAL. 20 specimens collected by the author from the type locality, British Museum (Nat. Hist.) nos. BB. 45710-19, BB. 45770-79 ; 30 specimens from near Bourges (Cher) collected by M. Delance, (University of Dijon).

DESCRIPTION. *External characters.* The species is an ordinary looking rhyrchonellid with the valves either equally biconvex or with the brachial valve slightly the more inflated. Length and width are about equal and either may be the greater; maximum width may be well toward the anterior or roughly median, thus giving a considerable range of overall outline. The young specimens are more flattened and subtriangular.

Most specimens have a high, strong beak which is flanked by strong beak ridges. The interarea is markedly incurved and is developed most strongly at the base of the beak where it impinges on the brachial valve giving a distinctive bend to the hinge line. A large, circular, hypothrydid pedicle opening is present and is limited by conjunct deltidial plates.

The radial ornament consists of rather coarse, steep, simple ribbing, while the concentric ornament comprises numerous very fine growth lines. The anterior commissure either shows a symmetrical low uniplication or varying degrees of asymmetry ; the latter feature is never so strongly developed as in *Torquirhynchia*, but shows the same sort of variation as described for *Septaliphoria*.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.26 cm	0.51 cm	1.25 cm
1.82 cm	0.77 cm	1.66 cm
2.40 cm	1.85 cm	2.17 cm
2.28 cm	1.42 cm	2.18 cm
2.50 cm	1.78 cm	2.20 cm

Internal characters. Pedicle valve. The beak is massive and the sub-parallel dental lamellae are quite short resulting in the development of only small lateral cavities. A small pedicle collar is present. The teeth are strong and crenulated and the species also possesses strong inner and outer socket ridges.

Brachial valve. The hinge plates are arched ventrally and the inner hinge plate is distinctive in showing a dorsally directed ridge flanked by small septalial plates. Crural bases are differentiated ; the relatively small radulifer crura curve slightly toward the ventral valve.

DISTRIBUTION. Only known from the type locality and from near Bourges (Cher), France.

OCCURRENCE. The specimens from Isère were collected from a band of fine-grained limestone, about 1.25 m thick, in which they occurred as loose groups. The associated fauna consisted of occasional zeilleriids and lamellibranchs, including oysters. M. Delance, of the University of Dijon, describes his material as coming from a "calcaire crayeux blanc, très friable", which lies above a massive reef limestone containing corals.

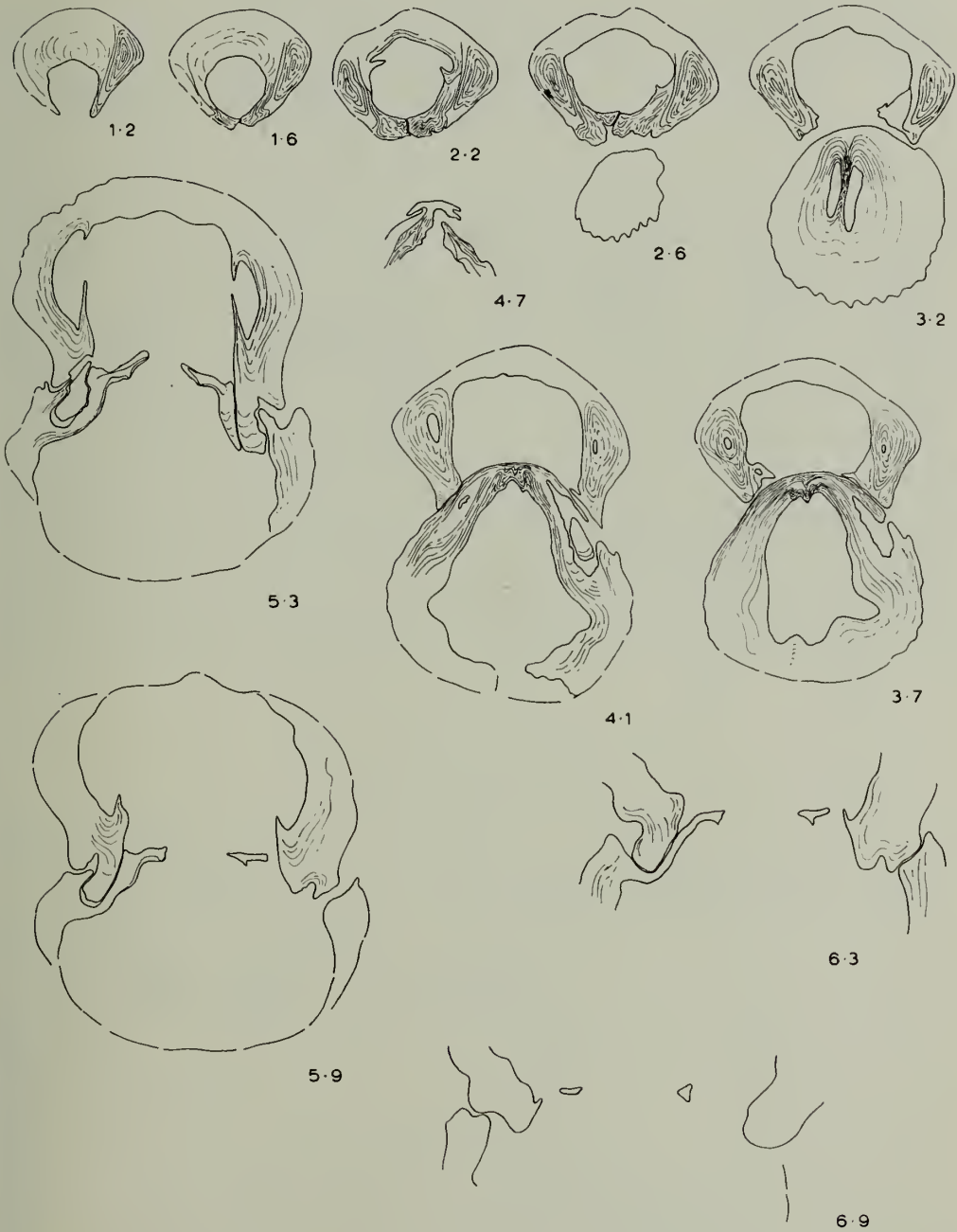


FIG. 38. Transverse serial sections of "*Rhynchonella*" *ordinaria* sp. nov. Topotype. Oxfordian—*pseudocordata* zone. Mont Dolet (Isère), France. ($\times 3$).

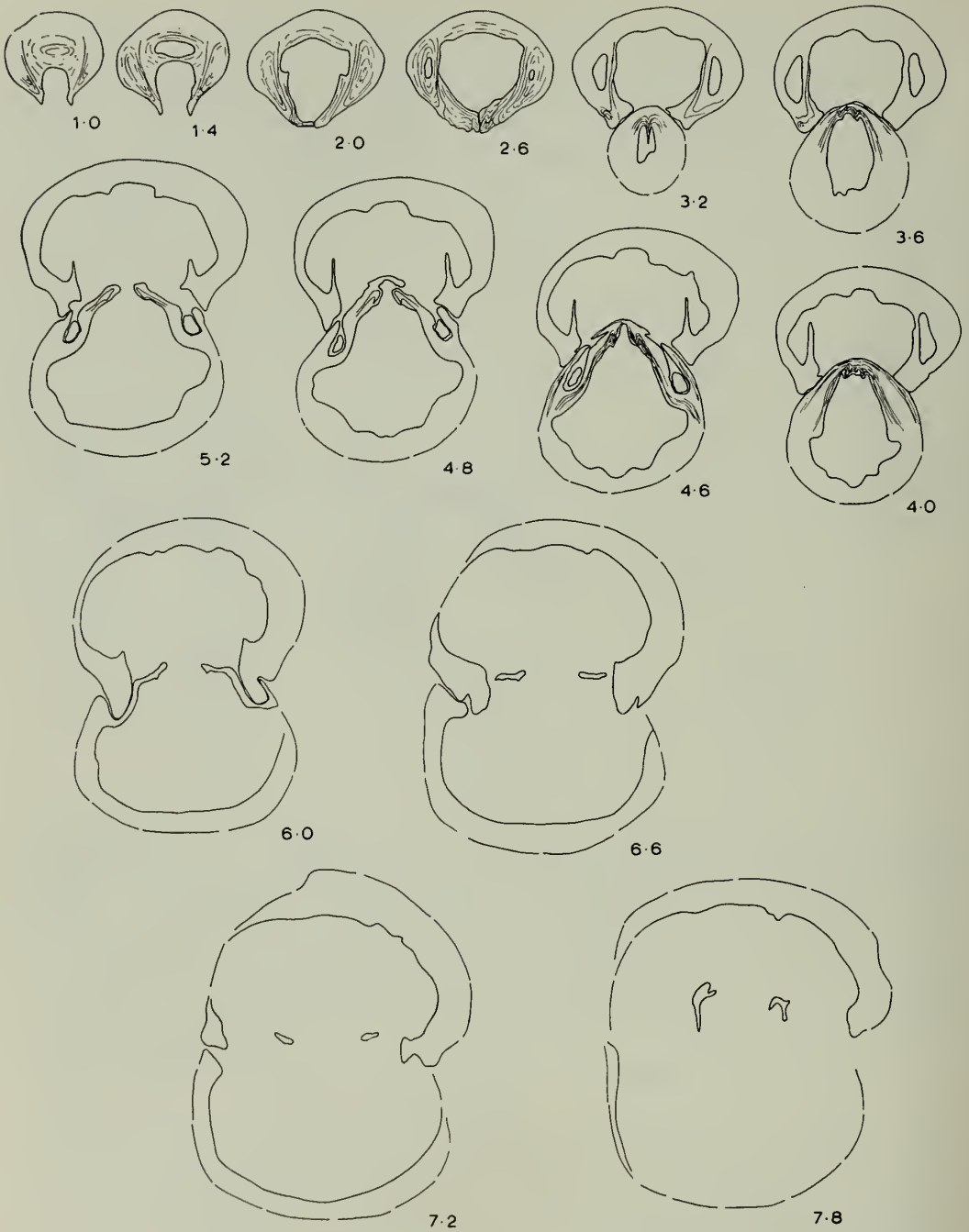


FIG. 39. Transverse serial sections of "*Rhynchonella*" *ordinaria* sp. nov. "Sequanien", Bourges (Cher), France. ($\times 4$).

REMARKS. Externally, the species appears similar to forms such as "*R.*" *hopkinsi* of the Bathonian which are normally referred to *Burmirhynchia* Buckman. However, there is considerable doubt as to many of the features of that genus and nobody appears to have published serial sections of topotypic material. Mr. E. F. Owen has kindly allowed the author to see sections of a Burmese specimen in the reference collection of the B.M.(N.H.), and while those seem to be closely comparable with those made of "*R.*" *ordinaria*, this in itself is somewhat odd in view of the original description of the genus in which Buckman stressed the prominent nature of the median septum and dental lamellae, features only poorly developed in "*R.*" *ordinaria*. These latter features can be clearly seen in the burnt specimens figured by Buckman (1918) and are also in a specimen attributed to *R. hopkinsi* from Chatillon-sur-Seine, which was sectioned for comparison. Although it is very difficult to judge to what extent such features observed externally will be developed as seen in transverse section, it is considered that their very weak development in "*R.*" *ordinaria* represents a marked discrepancy as compared with the species figured as *Burmirhynchia* by Buckman.

In general shape and form of ribbing, "*R.*" *ordinaria* is also comparable with certain species of the genus *Kallirhynchia* Buckman. Internally, it shows some resemblance to *Kallirhynchia yaxleyensis*, as figured by Muir-Wood (1934), especially in the development of its septalial plates and in the shape of the crura. However, *Kallirhynchia*, as it is at present defined, is restricted to the Bathonian and consequently it seems unwise to place *ordinaria* in that genus until intermediate forms have been described. At present the rhynchonellid faunas of the Bathonian and Callovian are very imperfectly known.

"*Rhynchonella*" *pyrenaei* sp. n.

(Pl. 3, fig. 7, text-fig. 40)

NAME. Latin—Pyrenaeum-i, the Pyrenees; the type locality is near Pau (Basses-Pyrénées).

DIAGNOSIS. Small to medium sized rhynchonellid; length greater than width; beak relatively large and suberect; about twelve ribs, some of which bifurcate; low uniplication; crura radulifer.

STRATIGRAPHICAL RANGE. Lower Oxfordian.

TYPE SPECIMEN. Holotype from the Pic du Gar near Pau (Basses-Pyrénées). BB. 45161.

MATERIAL. Large number of broken and poorly preserved specimens in the author's collection.

DIMENSIONS OF HOLOTYPE. Length 1.51 cm, thickness 0.87 cm, width 1.29 cm; this is the only specimen figured, B.M. BB.45161.

DESCRIPTION. *External characters.* The beak ridges and interarea are only weakly developed. The material was not sufficiently well preserved to allow the elucidation of the details of the pedicle opening and the deltidial plates. Concentric ornament was only observed on one specimen and consisted of growth lamellae.

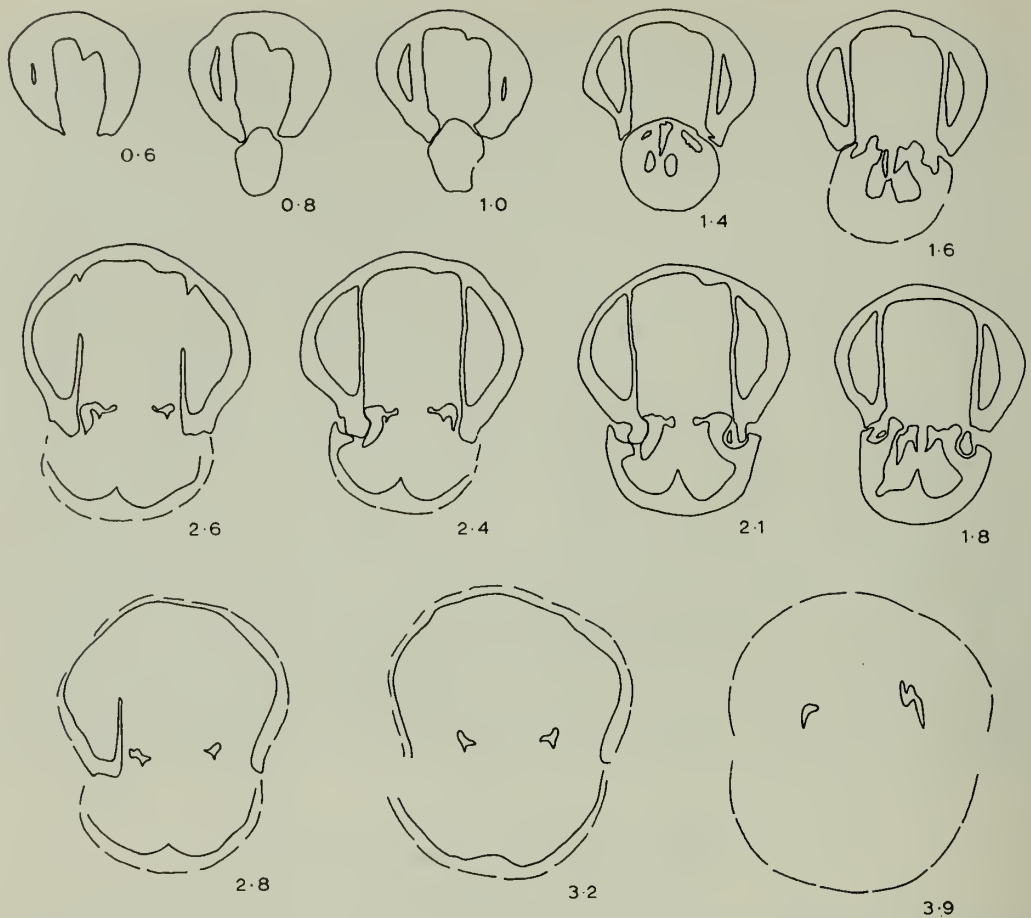


FIG. 40. Transverse serial sections of "*Rhynchonella*" *pyrenaei* sp. nov. Topotype. Oxfordian. Pic du Gar, (Basses Pyrénées), France. ($\times 5$).

Internal characters. Pedicle valve. The delthyrial cavity is subquadrate and limited by long, strong dental lamellae. Inner socket ridges are well developed; lateral denticulae are present.

Brachial valve. The median septum is strong and long septalial plates are developed. As seen in transverse section, the crura possess a very distinctive appearance through having "knob-like" structures median of the sharply pointed crural bases.

DISTRIBUTION. Only known from the type locality.

OCCURRENCE. All the material came from a bed about 10 cm thick where the species occurred profusely together with a lesser number of terebratulids. The matrix consisted of a very hard, dark limestone from which it was very difficult to extract specimens.

REMARKS. The species has not been referred to a genus as it is markedly dissimilar to any other species known to the author occurring in the Oxfordian. The distinctively shaped crura are closely comparable to those of *Prionorhynchia serrata* (J. de C. Sowerby) figured by Ager (1956) ; however, there is little resemblance externally and the latter is only known from the Lower Jurassic.

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PLATE 1

All specimens are figured natural size.

In all cases: a=dorsal view. b=lateral view. c=anterior view. d=posterior view.

FIGS. 1 a-d. *Monticlarella striocincta* (Quenstedt). Kimmeridgian—*cymodoce* zone. (Bedded Virieu Limestone), N. of Lac d'Armaille (Ain), France. Collection of the Geology Dept. of Imperial College, London.

FIGS. 2 a-d. *M. striocincta* (Quenstedt). Oxfordian ("Malm alpha"). Lochengründle, Germany. Collection of the University of Tübingen.

FIGS. 3 a-d. *M. striocincta* (Quenstedt). Details as fig. 2.

FIGS. 4 a-d. *Monticlarella czenstochaviensis* (Roemer). Oxfordian. Holy Cross Mountains, Poland. Collection of Dr. D. V. Ager.

FIGS. 5 a-d. *Monticlarella triloboides* (Quenstedt). Kimmeridgian, ("Weisser Jura delta"). "Schwäbische Alb". Collection of the University of Tübingen.

FIGS. 6 a-d, 7 a-d. *M. triloboides* (Quenstedt). Details as for fig. 5.

FIGS. 8 a-d. *Monticlarella strioplicata* (Quenstedt). Kimmeridgian, ("Malm delta"). Barrenberg, Germany. B.M. BB. 44130.

FIGS. 9 a-d. *M. strioplicata* (Quenstedt). Details as fig. 8. B.M. BB. 44131.

FIGS. 10 a-d. *M. strioplicata* (Quenstedt). Details as fig. 8. B.M. BB. 44132.

FIGS. 11 a-d. *Lacunosella arolica* (Oppel). Oxfordian, *transversarium* zone. Jura meridionale, France. B.M. BB. 44134.

FIGS. 12 a-d. *L. arolica* (Oppel). Oxfordian, ("Birmensdorfer Schichten"), Birmensdorf, Switzerland. B.M. BB. 44133.

FIGS. 13 a-d. *Lacunosella pseudodecorata* (Rollier). ?"Weis Jura gamma". ?Tieringen. Collection of the University of Tübingen.

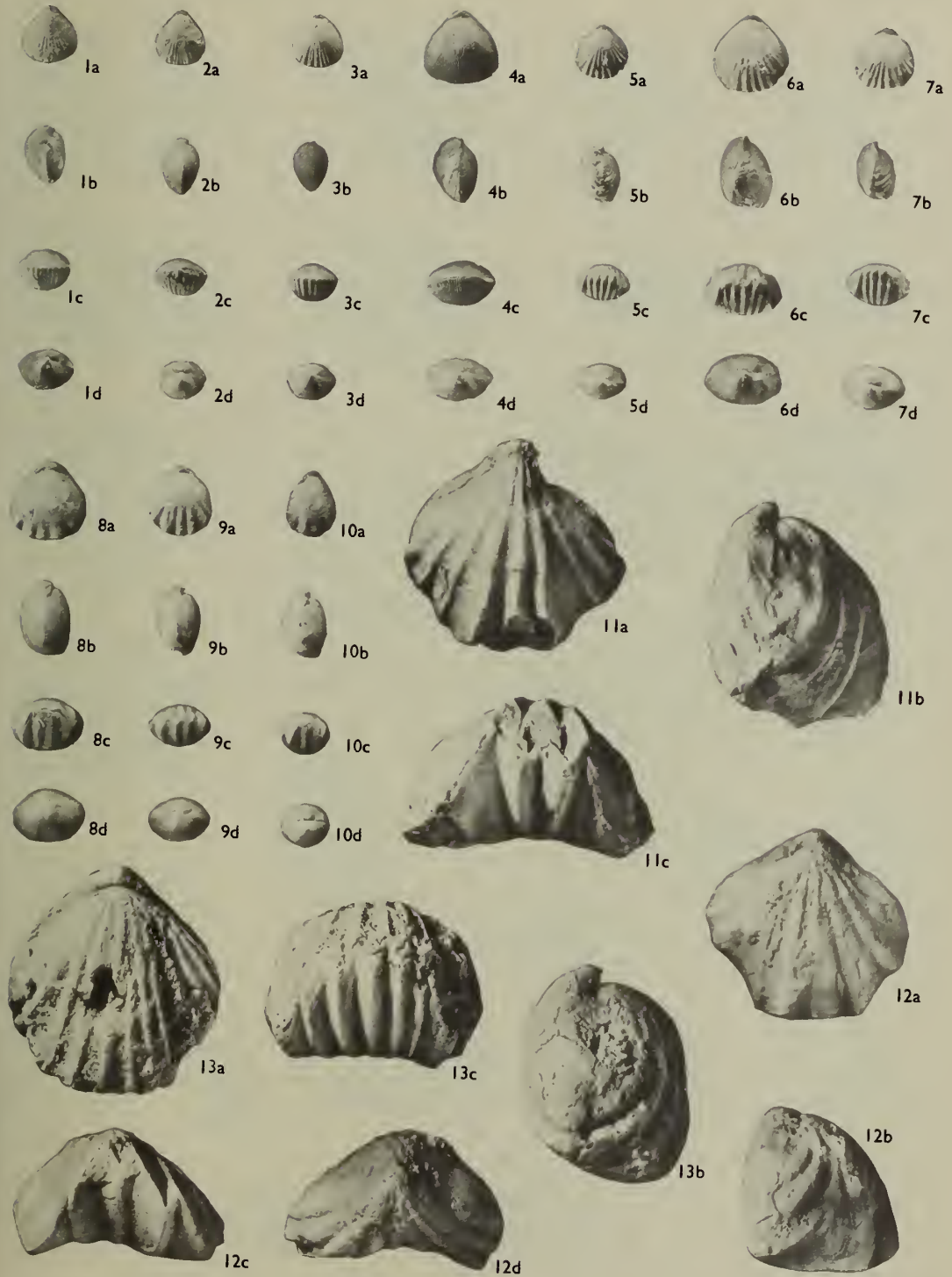


PLATE 2

FIGS. 1 a-d. *Lacunosella vaga* sp. nov. Holotype. Kimmeridgian, *mutabilis* zone. Sermérieu (Isère), France. B.M. BB. 44135.

FIG. 2. *L. vaga* sp. nov. Paratype. Details as fig. 1. B.M. BB. 44136.

FIGS. 3 a-d. *L. vaga* sp. nov. Paratype. Kimmeridgian, ("Malm delta"). Lahm-Köttel, Germany. B.M. BB. 44137.

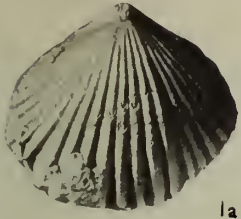
FIGS. 4 a-d. *Lacunosella selliformis* (Lewiński). Oxfordian. Tokarnia near Checiny, Poland. B.M. BB. 44142.

FIGS. 5 a-d. *Lacunosella cracoviensis* (Quenstedt). Upper Oxfordian-Lower Kimmeridgian, ("Malm beta/gamma"). Würgau, Germany. B.M. BB. 44138.

FIGS. 6 a-d. *L. cracoviensis* (Quenstedt). Details as fig. 5. B.M. BB. 44139.

FIGS. 7 a-d. *Lacunosella sparsicosta* (Quenstedt). Kimmeridgian, ("Malm gamma"). Barrenberg, Germany. B.M. BB. 44140.

FIGS. 8 a-d. *L. sparsicosta* (Quenstedt). Details as fig. 7. B.M. BB. 44141.



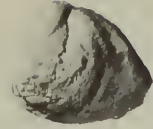
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1b



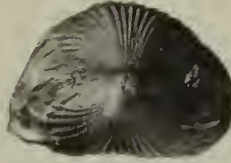
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4b



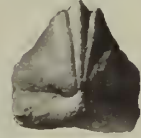
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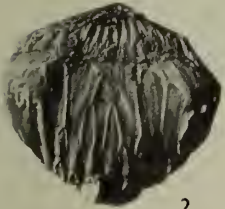
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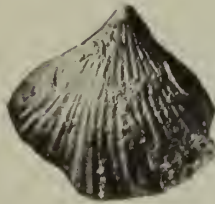
4c



4d



2



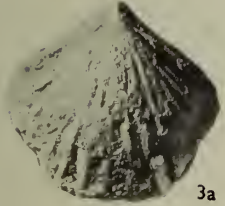
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5b



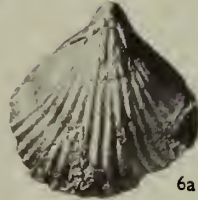
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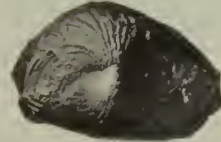
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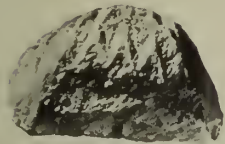
3b



6a



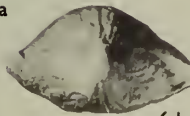
5d



3c



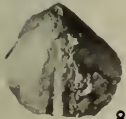
6c



6d



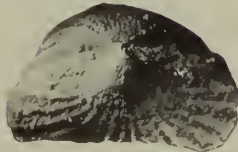
6b



8a



8b



3d



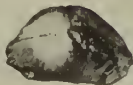
7a



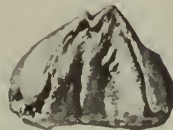
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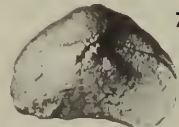
8c



8d



7c



7d

PLATE 3

FIGS. 1 a-d. *Lacunosella multiplicata* (Quenstedt). "Weiss Jura gamma". Thieringen, Germany. Collection of the University of Tübingen.

FIGS. 2 a-c. *Lacunosella trilobataeformis* Wiśniewska. "Malm alpha/beta". Rüsselbach bei Grafenberg, Germany. B.M. BB. 45160.

FIG. 3. *Lacunosella trilobata* (Zieten). Lower Volgian, ("Malm epsilon"). Wittislingen, Germany. B.M. BB. 44143.

FIGS. 4 a-d. *L. trilobata* (Zieten). "Kimmeridgien". Steinweiler bei Nattheim, Germany. Collection of the Naturhistorisches Museum, Basel. no. L 1691.

FIGS. 5 a-c, 6 a-d. *L. trilobata* (Zieten). Details as fig. 3. B.M. BB. 44144-5.

FIGS. 7 a-d. "*Rhynchonella*" *pyrenaei* sp. nov. Holotype. Oxfordian. Pic du Gar near Pau (Basses Pyrénées), France. B.M. BB. 45161.

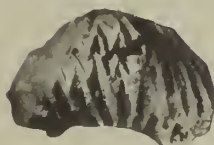
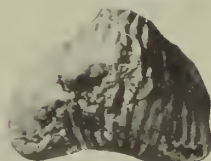
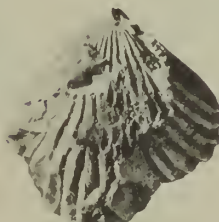
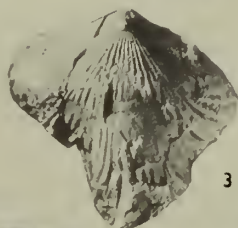
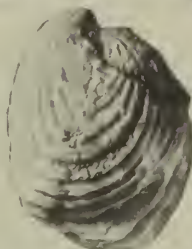
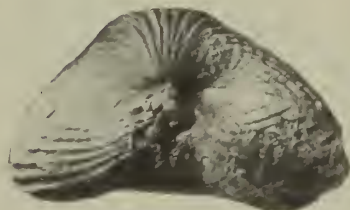
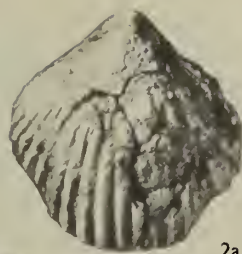
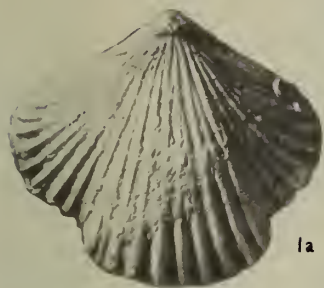


PLATE 4

FIGS. 1 a-d. *Rhynchonella portlandica* Blake. Paratype. Lower Volgian, (Lower Portland Sand). St. Alban's Head, Dorset, England. B.M. B. 52284.

FIGS. 2 a-d. *R. portlandica* Blake. Holotype. Details as fig. 1. B.M. B. 52283.

FIGS. 3 a-d. *Rhynchonella loxiae* Fischer. Upper Volgian. Khoroshevo near Moscow. Collection of Dr. D. V. Ager.

FIGS. 4 a-b. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (Portland Sands). Ringstead Bay, Dorset, England. B.M. B. 72240.

FIGS. 5 a-d. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (Basal Shell Bed, Portland Limestone). Cliff N.W. of Portland, England. Collection of the University Museum, Oxford. J. 1006.

FIGS. 6 a-d, 7, 8. *Rhynchonella* sp. Kimmeridgian, ?*pseudomutabilis* zone, (Boulder Beds). West Garty, Sutherland, Scotland. B.M. BB. 44146-7, 45162.

FIGS. 9 a-c, 10 a-d, 11 a-d, 12 a-d. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (Upper Blacknore Beds). West Weare Cliffs, Portland, England. Collection of the University Museum, Oxford. J. 2462.

FIGS. 13 a-d, 14 a-d. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (upper part of Portland Sand). Foot of Gad Cliff, Dorset, England. Collection of the University Museum, Oxford. J. 167.

FIGS. 15 a-d. *Rhynchonella* cf. *R. subvariabilis* Davidson. Lower Volgian, (top of Kimmeridge Clay just below Portland Sands Passage Beds). Chapman's Pool, Dorset, England. B.M. B. 47251.

FIGS. 16 a-d. *Rhynchonella* cf. *R. subvariabilis* Davidson. Lower Volgian, (Kimmeridge Clay, about 40' below *rotundum* nodules). Chapman's Pool, Dorset, England. Collection of the Sedgewick Museum, Cambridge. J. 1500.

FIGS. 17 a-d. *Rhynchonella* cf. *R. sarapaulensis* Makridin. Lower Volgian, (Kimmeridge Clay, *rotundum* nodules). Chapman's Pool, Dorset, England. Collection of the Sedgewick Museum, Cambridge. J. 1512.

FIGS. 18 a-d. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (Lyddite Bed, Portland Beds). Long Crendon, Buckinghamshire, England. Collection of the Sedgewick Museum, Cambridge. J. 1524.

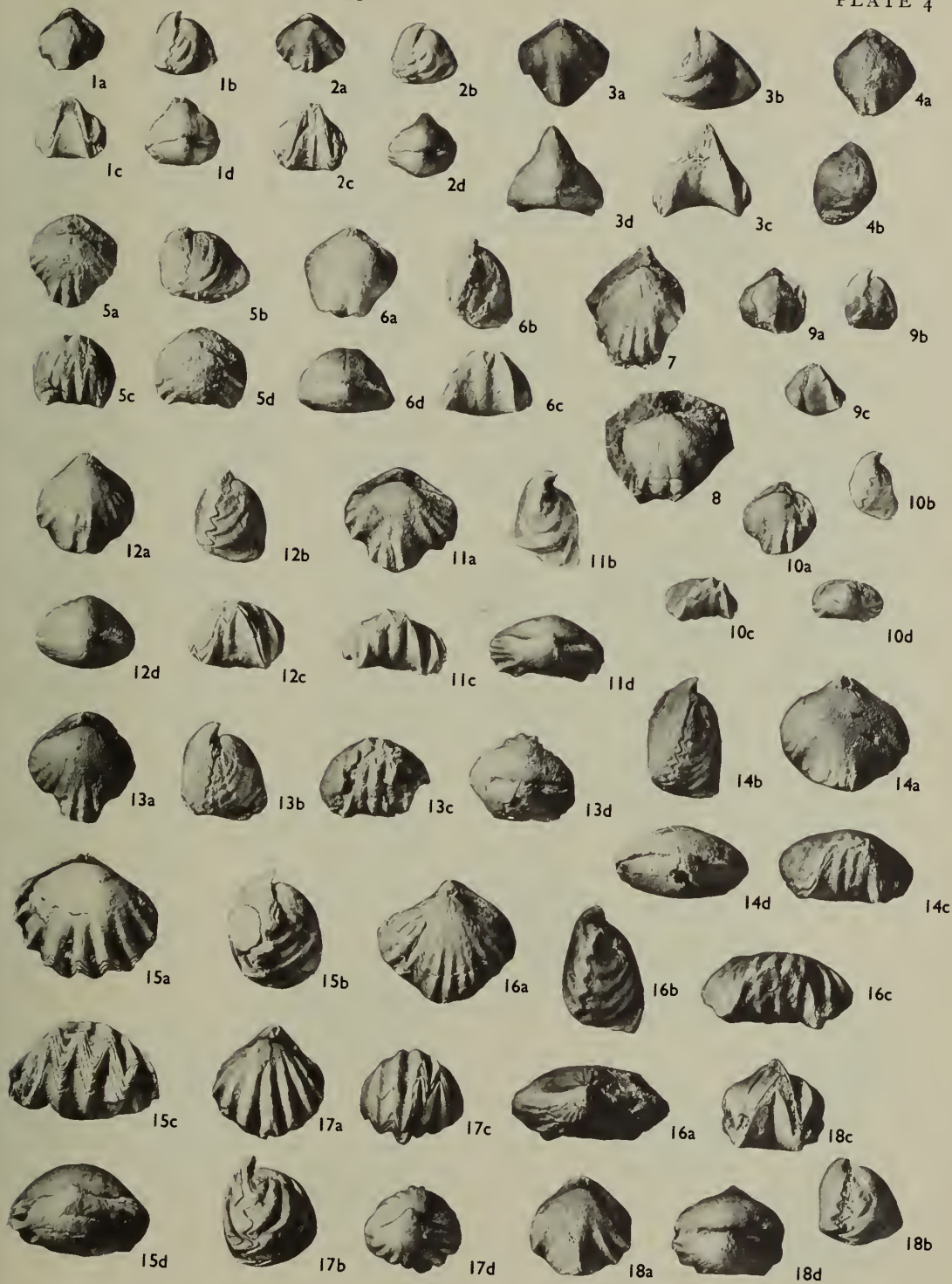


PLATE 5

- FIGS. 1 a-d, 2 a-d. *Rhynchonella* sp. Callovian. Wrzova, Poland. B.M. BB. 44148-9.
- FIGS. 3 a-d, 4 a-d, 5, 6. *Rhynchonella riveleensis* Loriol. Upper Oxfordian. Alex near Oyonnax (Ain), France. B.M. BB. 44150-53.
- FIGS. 7 a-d, 8 a-d, 9 a-c. *Thurmannella obtrita* (Defrance). Oxfordian, (Terrain à Chailles). Pagny-sur-Meuse (Meurthe et Moselle), France. B.M. BB. 44154-56. Figs. 8 a-d neotype.
- FIGS. 10 a-d. *Thurmanella acuticosta* sp. nov. Oxfordian, (Lower Calcareous Grit). Filey Brigg, Yorkshire, England. Holotype. B.M. BB. 44158.
- FIGS. 11 a-d. *T. acuticosta* sp. nov. Paratype. Details as fig. 10. B.M. BB. 44157.
- FIGS. 12 a-d. *Acanthothiris spinosa* (Linnaeus). Neotype. Bajocian, (Upper *Trigonia* or *Clypeus* Grit). Rodborough Hill, Gloucs., England. B.M. BB. 45400.
- FIGS. 13 a-d. *A. spinosa* (Linnaeus). Bajocian, (Upper *Trigonia* or *Clypeus* Grit). Stroud, Gloucs., England. B.M. B. 63318.
- FIGS. 14 a-d. *A. spinosa* (Linnaeus). Juvenile specimen. Bajocian, (Upper *Trigonia* Grit). Waterworks Quarry, Wootton under Edge, Gloucs., England. B.M. BB. 44162.
- FIG. 15. *A. spinosa* (Linnaeus). Crushed specimen showing spines attached. Upper Bathonian, ("Varians Schichten"). Liestal near Basel, Switzerland. B.M. BB. 44160.
- FIGS. 16 a-d, 17 a-d. *A. spinosa* (Linnaeus). Details as fig. 15. B.M. BB. 44161 and 44159.

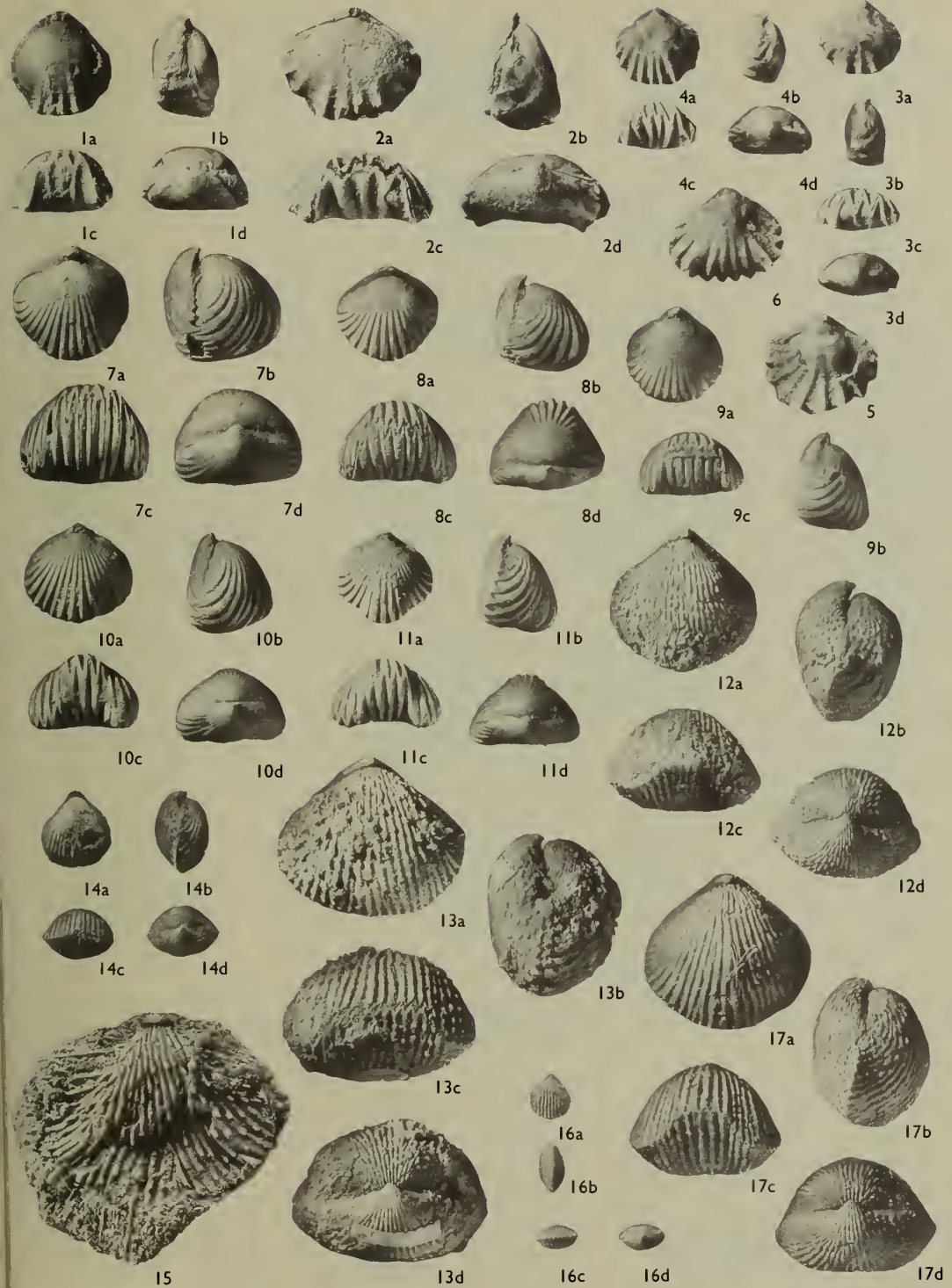


PLATE 6

FIGS. 1 a-d. Plaster cast of the type specimen Orbigny's *Acanthothiris costata* the original is in the collection of Jardin des Plantes (Musée d'histoire Naturelle), Paris. This specimen was figured by Thevenin (1910).

FIGS. 2 a-d, 3 a-d, 4 a-d. *Acanthothiris* cf. *A. costata* Orbigny. Upper Bajocian-Lower Callovian (Chanaz Beds). Pugieu (Ain), France. B.M. BB. 44163-65.

FIGS. 5 a-d. *Acanthorhynchia* (*Acanthorhynchia*) *panacanathina* (Buckman & Walker). Bajocian, zigzag zone. Burton Bradstock, Dorset, England. B.M. B. 63479.

FIGS. 6 a-d. *A. (Acanthorhynchia) panacanathina* (Buckman & Walker). "Inferior Oolite". Larkfield Quarry, Burton Bradstock, Dorset, England. B.M. B. 31306.

FIGS. 7 a-d. *A. (Acanthorhynchia) panacanthina* (Buckman & Walker). Bajocian, parkinsoni zone. Wennet Hills, Burton Bradstock, Dorset, England. B.M. B. 31304.

FIGS. 8 a-d. *Acanthorhynchia* (*Acanthorhynchia*) *spinulosa* (Oppel). "Oxfordien". Montsaon, Chaumont (Haute Marne), France. B.M. B. 36080.

FIGS. 9 a-d. *A. (Acanthorhynchia) spinulosa* (Oppel). "Oxfordien". Bolognes (Haute Marne), France. B.M. B. 36079.

FIGS. 10 a-d. *Acanthorhynchia* (*Acanthorhynchia*) *vilsensis* sp. nov. Paratype. Callovian. Legam bei Vils, southern Germany. Collection of the Bayerische Staatsammlung für Paläontologie und historische Geologie, München. AS xxiv 5.

FIGS. 11 a-d. *A. (Acanthorhynchia) vilsensis* sp. nov. Holotype. Details as fig. 10. AS xxiv 2.

FIGS. 12 a-d. *A. (Acanthorhynchia) vilsensis* sp. nov. Paratype. Details as fig. 10. AS xxiv 5.

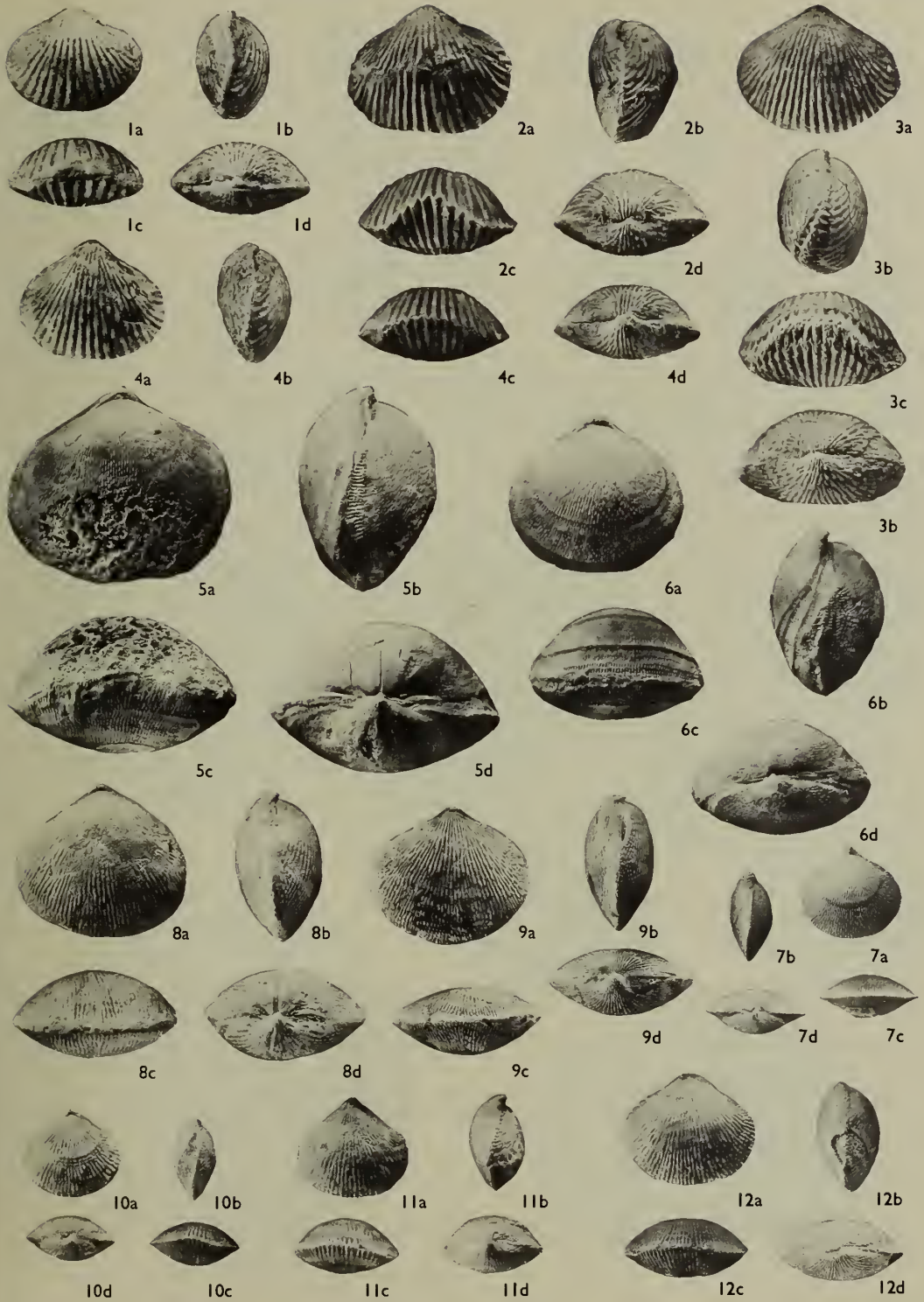


PLATE 7

FIGS. 1 a-d. *Acanthorhynchia (Echinirhynchia) senticosa* (Schlotheim). Neotype. "Weissem Jura". Amberg, Germany. Figured by Rothpletz (1886). Collection of the Bayerische Staatsammlung für Paläontologie und historische Geologie, München. AS vii 330.

FIGS. 2 a-d, 3 a-d. *A. (Echinirhynchia) senticosa* (Schlotheim). "Malm delta". Heiligenstadt near Erlangen, Germany. Collection of the Geologisches Institut der Universität, Erlangen.

FIGS. 4 a-d, 5, 6. *Acanthorhynchia (Echinirhynchia) fileyensis* (Buckman & Walker). Oxfordian, (Lower Calcareous Grit). Filey, Yorkshire, England. B.M. B. 31867, B. 31334, B. 31333.

FIGS. 7 a-d. *Acanthorhynchia (Echinirhynchia) lorioli* (Rollier). Oxfordian, (Terrain à Chailles). Fringeli, "Berner Jura". Collection of the Naturhistorisches Museum, Basel. L 1700.

FIGS. 8 a-d, 9. *A. (Echinirhynchia) lorioli* (Rollier). Oxfordian, *transverarium* zone. St. Sorlin, Liefnans (Jura), France. B.M. BB. 44166-67.

FIGS. 10 a-b, 11 a-d. *Acanthorhynchia* sp. Upper Kimmeridgian, (Oignon Limestone). Colomieu (Ain), France. B.M. BB. 44169, 44168.

FIGS. 12 a-d, 13, 14, 15, 16. *Somalirhynchia sutherlandi* (Davidson). Topotypes. Kimmeridgian, *?pseudomutabilis* zone (Boulder Beds). West Garty, Sutherland, Scotland. Collection of the Geological Survey of Great Britain (Edinburgh Office). Fig. 12 no. G.S.E. 3684, West Garty; fig. 13 no. M 2268g, West Garty; fig. 14 no. G.S.E. 3681, West Garty; fig. 15 no. G.S.E. 3685, West Garty; fig. 16 no. G.S.E. 3686, Portgower.

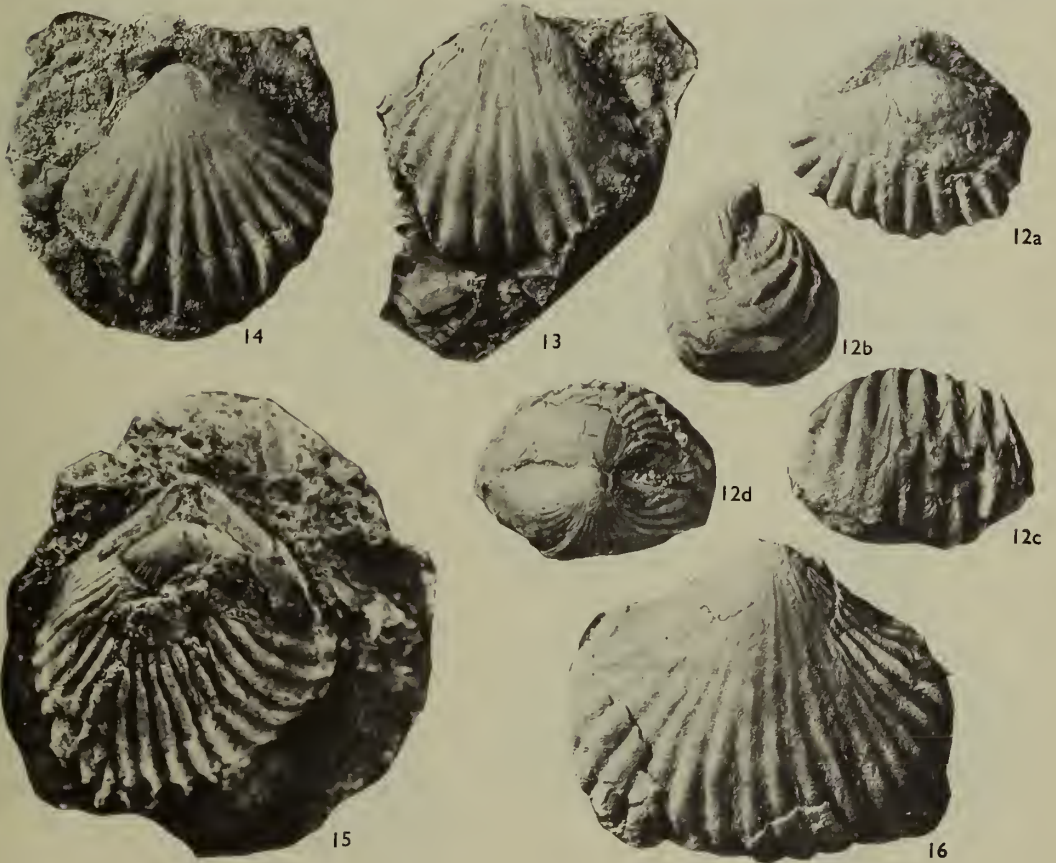
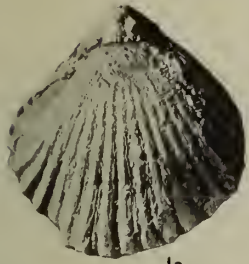


PLATE 8

FIGS. 1 a-d, 2 a-d, 3. *Somalirhynchia moeschi* (Haas). Oxfordian, *pseuoacordata* zone. Rochers de Fresnois, Chaumont, près Saint-Claude (Jura), France. B.M. BB. 44170-72.

FIGS. 4 a-d, 5 a-d. *Septaliphoria arduennensis* (Oppel). Oxfordian, (Terrain à Chailles). Pagny-sur-Meuse (Meurthe et Moselle), France. Fig. 4 neotype. B.M. BB. 44173-74.

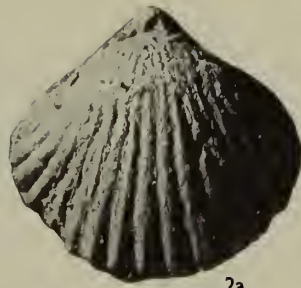
FIGS. 6 a-d, 7 a-d. *Septaliphoria?* *septentrionalis* sp. nov. ?Upper Oxfordian-?lower Kimmeridgian, (Alt-na-Cuile Sandstone). Alt-na-Cuile, Sutherland, Scotland. Fig. 6 holotype; fig. 7 paratype. B.M. BB. 44175-76.



1a



1b



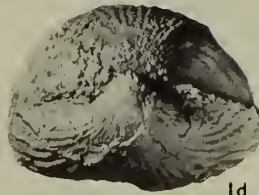
2a



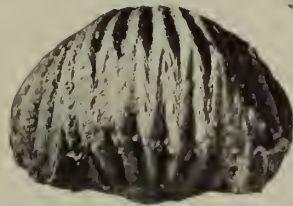
2b



1c



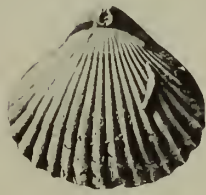
1d



2c



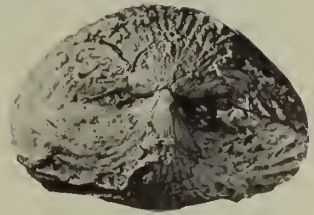
3



5a



5b



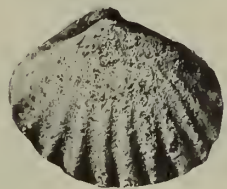
2d



5c



5d



7a



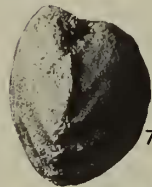
4a



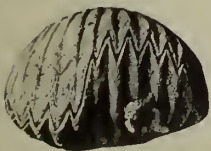
4b



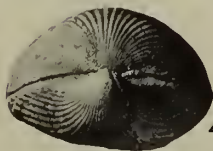
7c



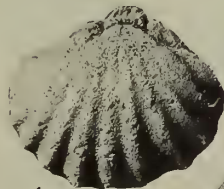
7b



4c



4d



6a



6c



6b

PLATE 9

FIGS. 1 a-d, 2 a-c, 3 a-c, 4. *Septaliphoria? hudlestoni* (Rollier). Topotypes. Kimmeridgian, (Abbotsbury Ironstone). Abbotsbury, Dorset, England. B.M.

FIGS. 5 a-c, 6 a-d. *Septaliphoria paucicosta* sp. nov. Oxfordian, (Lower Calcareous Grit). Hutton Bushell, Beedale, Yorkshire.

FIG. 5. Paratype ; BB. 45395, fig. 6 holotype. B.M. BB. 45394.

FIGS. 7 a-d, 8 a-d, 10, 11. "*Rhynchonella*" *ordinaria* sp. nov. Paratypes. "Sequanien". Calliors du Chateau, Bourges (Cher), France. B.M. BB. 45163-66.

FIGS. 9 a-d. "*Rhynchonella*" *ordinaria* sp. nov. Holotype. Oxfordian, *pseudocordata* zone. Mont Dolet, Sermérieu (Isère), France. B.M. BB. 45167.

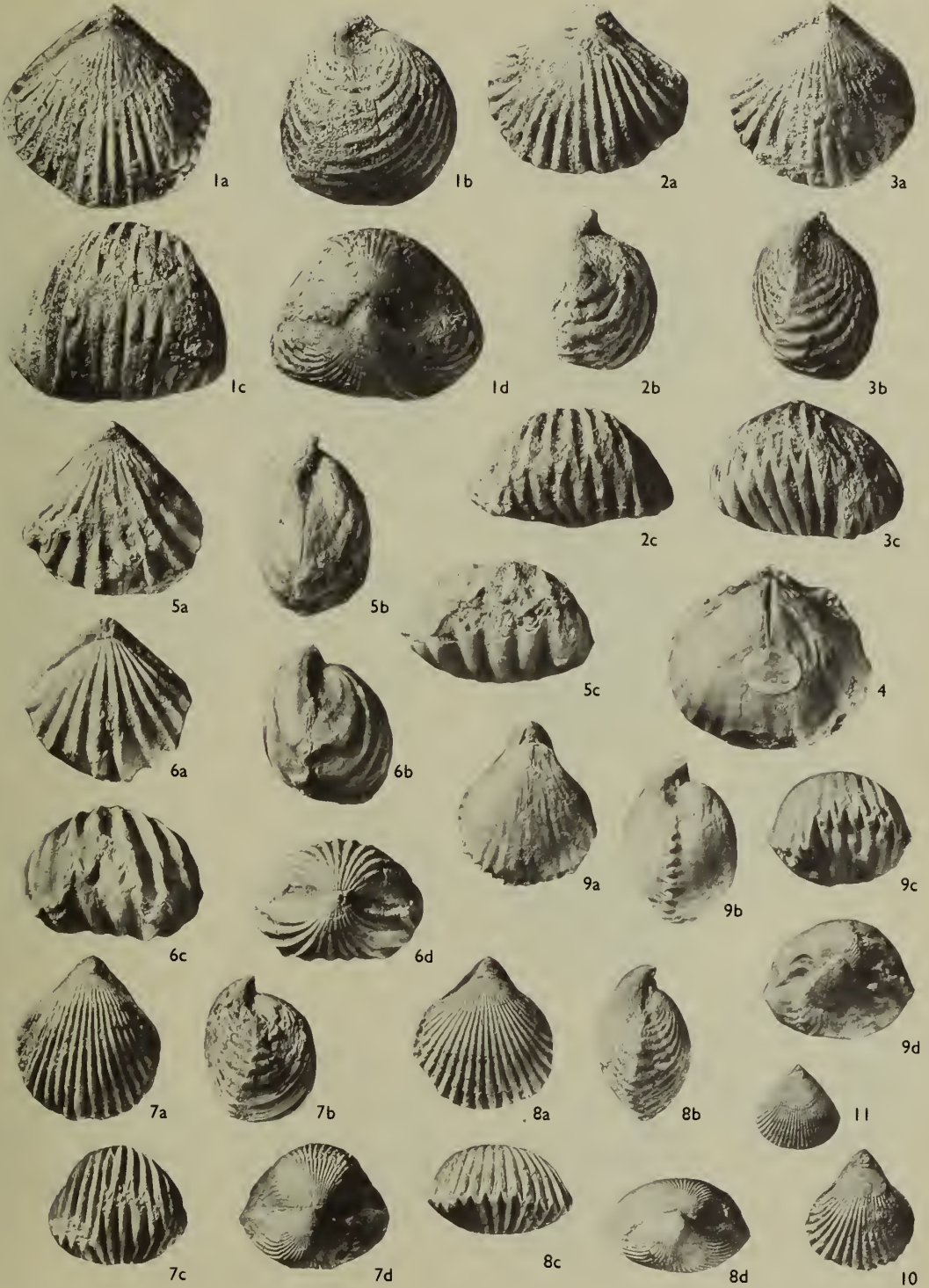


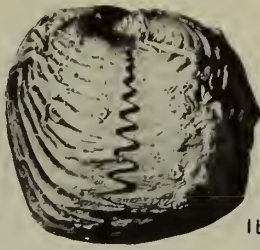
PLATE 10

FIGS. 1 a-d, 2 a-d, 3 a-d. *Torquirhynchia inconstans* (J. Sowerby). Topotypes. Kimmeridgian, *baylei* zone, (Kimmeridge Clay). Ringstead Bay, Dorset, England. B.M. BB. 44177-79.

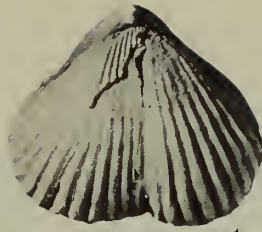
FIGS. 4 a-c, 5 a-d, 6. *Torquirhynchia guebhardi* (Jacob & Fallot). Kimmeridgian, *cymodoce* zone, (Bedded Virieu Limestone). N. of Lac d'Armaille (Ain), France. B.M. BB. 45168-70.



1a



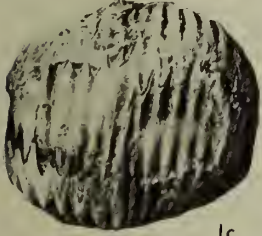
1b



4a



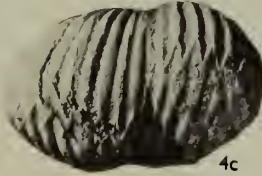
4b



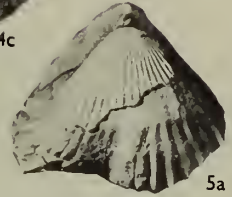
1c



1d



4c



5a



2a



2b



6



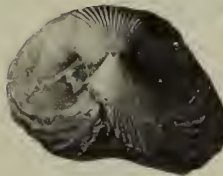
5b



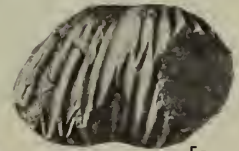
2c



2d



5d



5c



3a



3b



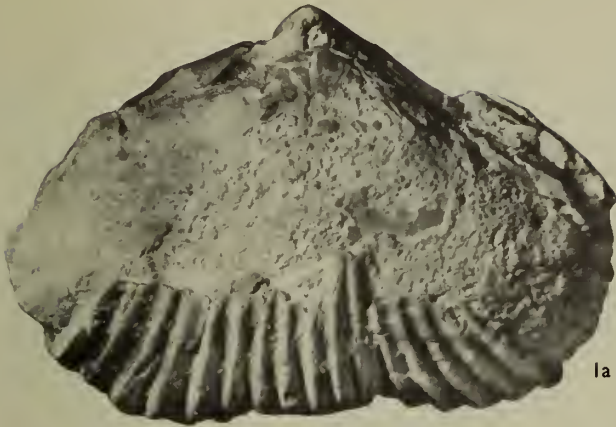
3d



3c

PLATE 11

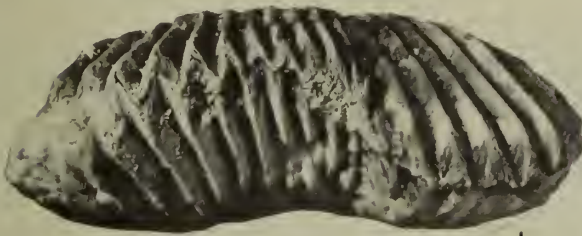
FIGS. 1 a-d, 2 a-d, 3 a-d. *Torquirhynchia speciosa* (Münster). Upper Kimmeridgian-Lower Volgian, ("Diceras-Kalk"). Saal near Ingolstadt, Germany. B.M. BB. 45171-73.



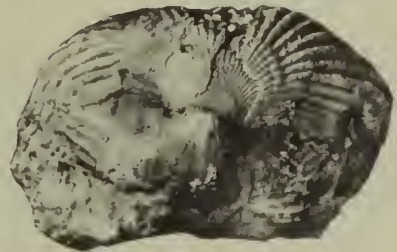
1a



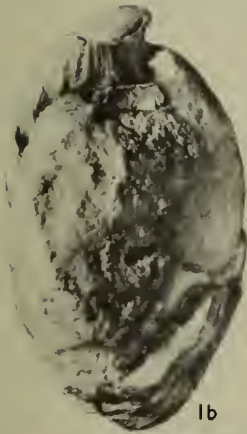
2a



1c



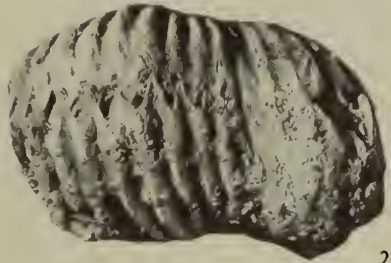
2d



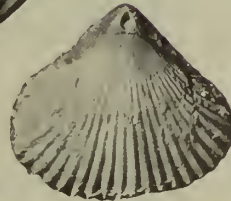
1b



2b



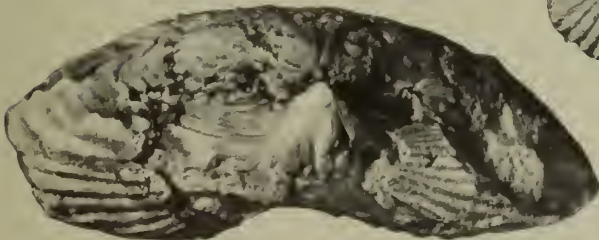
2c



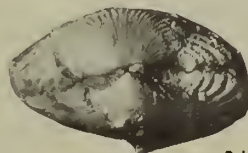
3a



3c



1d



3d



3b

PLATE 12

FIGS. 1 a-d, 2 a-d, 3 a-d. *Torquirhynchia* cf. *T. astieriformis* (Wiśniewska). Kimmeridgian, *mutabilis* zone. Sermérieu (Isère), France. B.M. BB. 45174-6.

FIG. 5. *Torquirhynchia inconstans* (Sowerby) from the Kimmeridge Clay of Ringstead Bay, Dorset. Shows the nature of the articulation, the shape of the median ridge and the outline of the muscle scars in the brachial valve. $\times 1\frac{1}{2}$. B. 60368.

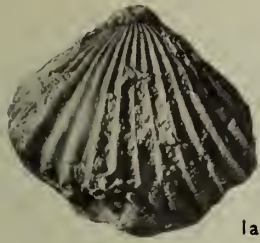
FIG. 4. Transverse through the hinge plate of *Septaliphoria paucicosta* sp. nov. showing the form of the septalial plate and the crural base. This is part of section 4, 3 figured in text-fig. 33. $\times 12$.

FIG. 6. Transverse section of *Septaliphoria paucicosta* sp. nov. showing the median septum and septalial plates. This is part of section 3, 4 in the series shown in text-fig. 33. $\times 5$.

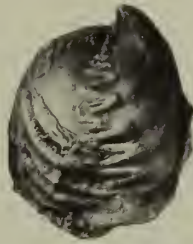
FIG. 7. Transverse section of *Acanthorhynchia (Acanthorhynchia) panacanthina* (Buckman & Walker) showing the thickened nature of the hinge plates. This is part of section 1, 9 in the series shown in text-fig. 24.

FIG. 8. Transverse section of *Zeilleria austriaca* (Zugmeyer) showing the form of the septalium. Specimen obtained from the Rhaetian of Piesting Tal, Lower Austria. The "peel" from which the photomicrograph was taken was kindly made available to the author by Dr. D. A. B. Pearson. $\times 5$.

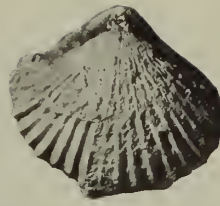
FIG. 9. Transverse through the hinge plates of *Lacunosella vaga* sp. nov. showing the form of the falcifer crura. This is part of section 3, 6 in the series shown in text-fig. 14.



1a



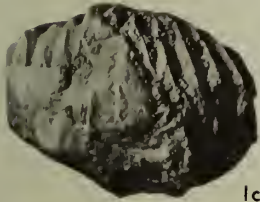
1b



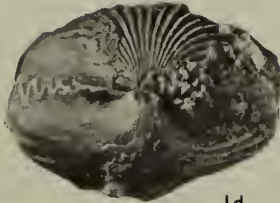
2a



2b



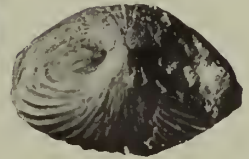
1c



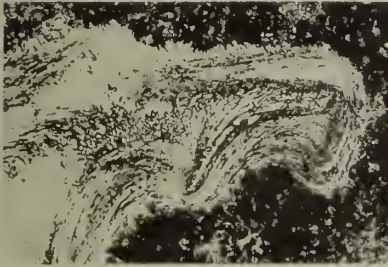
1d



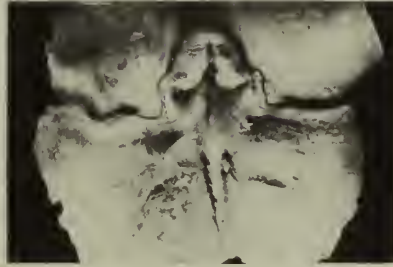
2c



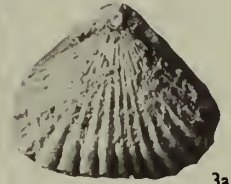
2d



4



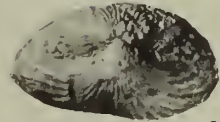
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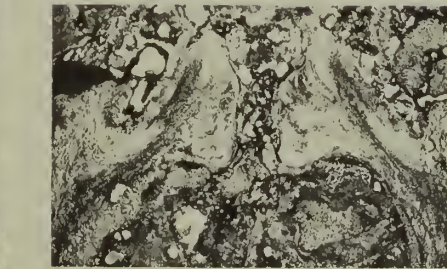
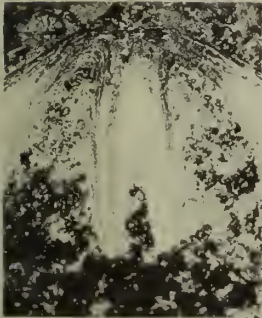
3a



3c



3d



7



6



8



9